# SPECIES TAXA. OF NORTHE AMERICAN BERDS A CONTRIBUTION TO COMPARATIVE SYSTEMATICS

ERNST MAYR

and

LESTER L. SHORT

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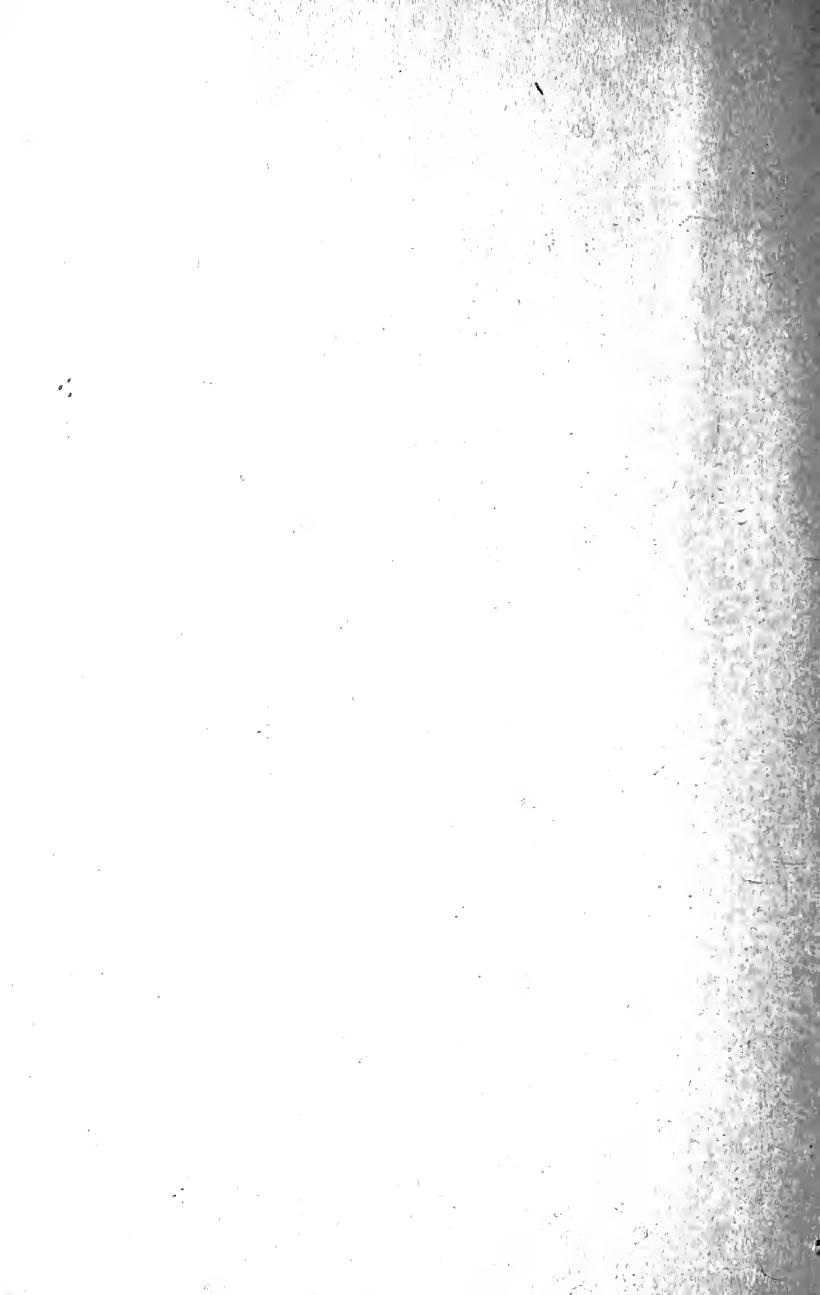
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#### SPECIES TAXA OF NORTH AMERICAN BIRDS

# A CONTRIBUTION TO COMPARATIVE SYSTEMATICS

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# A CONTRIBUTION TO COMPARATIVE SYSTEMATICS

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ERNST MAYR
Museum of Comparative Zoology

and

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Dedicated to
ERWIN STRESEMANN
leader in ornithological systematics
on the occasion of his 80th birthday
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#### I INTRODUCTION

It has long been known that many aspects of the genetic system of higher animals are different from those of higher plants. The reasons for these differences have been discussed in considerable detail by Stebbins (1950) and by Mayr (1963). However, there also has long been a feeling that even within each of the two kingdoms substantial differences exist among different groups of animals or of plants. To determine the nature and magnitude of such differences would seem to be one of the foremost tasks of comparative systematics, and yet this has not been done.

There are two reasons why there have been no such comparisons, despite their universally admitted value. One is that the level of maturity varies greatly in the taxonomy of different higher taxa; the second reason is that until quite recently very different species concepts were in vogue in diverse taxonomic groups.

One virtually unique pioneering contribution to comparative systematics was made by Verne Grant (1957: Table 1). He listed the frequency of "good" species in 11 large genera of Californian plants belonging to 11 different families. Of the 323 species included in these genera, 175 (54%) were considered good species by Grant. The designation "good species" refers to those that are clearly delimited from other species and whose recognition is not controversial among specialists. The various genera contain between zero and 100 percent good species. The special merits of Grant's analysis are twofold; it quantifies what previously had been expressed only in the vaguest terms; and, more importantly, it specifies the various biological reasons, e.g., cryptic species, hybridization, geographical isolates, for difficulties in making decisions when ranking species taxa (see below), and analyzes the contribution made by each of them.

No comparable investigations exist in animal taxonomy. Ornithologists generally take it for granted that species taxa are well defined, but critical, quantitative published data are lacking. Some other zoologists have made sweeping but unsupported claims such as that "the biological species has outlived its usefulness" and that "the idea of preponderance of good species in animals is a generality without foundation — an artifact of the procedures of taxonomy". However, it is equally possible that these claims themselves are artifacts of bad taxonomy.

The issue cannot be settled until taxonomists make the effort to present the actual data on which they base their claims. This is the principal objective of the present paper. There is a great need for truly comparative systematics, but—so far—the classification of natural taxa is sufficiently mature in only a few groups and regions to qualify as the basis for such

comparisons. The birds of North America (north of Mexico) clearly qualify and have, therefore, been chosen for an appropriate analysis. The *Check-list of North American Birds*, Edition 5 (1957) gives an up-to-date listing of species. It is used as a framework for the present analysis, and all modifications and additions are mentioned in a list of taxonomic comments.

## APPLICABILITY OF THE BIOLOGICAL SPECIES CONCEPT

In order to examine critically the question of whether or not the biological species concept has "outlived its usefulness," it is necessary to state first the meaning of the term "biological species concept." Species of inanimate objects are classes of "things." The appropriateness of assigning an object to one of these classes is determined by its similarity to other objects in this class. The biological species concept is a very different kind of concept. It is a relational concept, like the word "brother" (Mayr, 1963, 1969). A population belongs to a given species when not isolated from it by intrinsic reproductive barriers. The biological species concept has a meaning only for populations that coexist or are contiguous in space and time. Here it is self-operationally defined and it is only here that its application is truly important.

The question then is, quite simply, whether the biological species concept facilitates placing the multitude of local populations, varying in space and time, into well-defined monotypic or polytypic species taxa. The taxonomic status of coexisting forms can be determined without need for arbitrary decision. The assigning of populations from different localities to species taxa inevitably requires the drawing of inferences from the available evidence.

The delimitation of species, and the decision as to which isolated forms can be designated unequivocally as "good species" and which others are controversial, are somewhat subjective, at least in some cases. What we would like to have is a solid, quantitative answer to our question of how often the application of the biological species concept leads to difficulties, controversies, or ambiguities. Yet, even a quantitative answer, let us say the statement that "82 percent of the species of North American birds are unequivocally well delimited," is not enough. It would be merely a claim, unless backed by a tabulation of the original data. This is one of the reasons why we have presented in full the data on which our conclusions are based. This additionally permits the ecologist and the evolutionist to correlate the data with various aspects of the life cycle and of niche utilization. For instance, it permits one to investigate whether species structure and speciation are different in marine birds, fresh-water birds, large birds (of various sorts), and small song birds. Ecologists may also find our tabulation useful when making correlations with habitat preference, place in the ecosystem, rarity or commonness, size of clutch, life span, or other life history data in need of quantitative analysis.

The basic units for our analysis are the "zoogeographical species." These are either superspecies (Mayr, 1963; Amadon, 1966) or individual species not belonging to a superspecies. When several species comprise a superspecies, they are counted as *one* zoogeographical species just as is each individual species not forming part of a superspecies. All exceptions to this treatment are clearly indicated (as in Tables 3, 4, 5).

One fact must be thoroughly emphasized. A quantitative analysis, as presented in this paper, cannot be undertaken without being preceded by the most painstaking alpha taxonomy. It is first necessary to determine whether each species is geographically variable or not, and whether certain geographically isolated taxa are members of a polytypic species, of a superspecies, or of a species group. One must ask for each species "what is its nearest relative?" and "what degree of relationship is involved?" and the answers must be sought with a world-wide perspective as we have attempted herein. The importance of sound alpha taxonomy for ecological and evolutionary studies cannot be overemphasized. The raw material upon which our conclusions are based is presented in the two major components of this study, an analytical table (Table 1) listing the species taxa (Part III), and a set of taxonomic comments (Part III).

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#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA

Many bird species range widely and indeed some superspecies, particularly those of fresh-water birds, have cosmopolitan ranges. This contrasts strikingly with the situation in most genera of plants, lower vertebrates, and insects, many of which have extremely local ranges. Avian species become more nearly comparable to species in other groups of organisms when only their North American range is considered. For this reason all species have been tabulated and analyzed twice: once for their North American range and once for their total range.

The analytical table (Table 1) consists of seven columns. The first of these gives the scientific names of all the treated species, with the various "zoogeographic species" (see below) numbered consecutively within each family. The families are given identifying symbols (AA, AB, etc., see below). Superspecies are indicated by brackets, following Amadon (1966).

Every species is tabulated twice in Columns A through C, once with respect to its North American range (×), and again with respect to its total range (O). However, when a species falls within the same category for both its North American and its total range, only an "×" is used. Furthermore, if a species is endemic to North America (e.g., Aechmophorus occidentalis), the symbol "×e" is used ("e" for endemic). A "×" without an "e" indicates that the species may occur also outside North America but without changing its status (e.g., Podiceps auritus).

Monotypic species are scored in the second column, Column A. In the third column, Column B, those species are scored which are uncomplicated polytypic species, that is, those which are comprised of weakly to moderately differentiated subspecies, none of which pose taxonomic problems at the species level. If a widespread polytypic species is represented in North America by only a single subspecies, it is recorded as monotypic within North America, and entered with an "×" in Column A, and a "O" in either Column B or C (e.g., Gavia stellata).

In the fourth column, Column C, strongly differentiated polytypic species are recorded, that is, those which include subspecies so well marked that they have in the past been considered full species or are still so considered by some taxonomists. Allospecies, being members of superspecies, are listed in the fifth column, Column D.

In Column E a symbol indicates that the species listed at the left is one of several closely related species within its genus, considered as belonging to a species group (e.g., *Podiceps nigricollis*). The final column, headed "Remarks," lists under the appropriate column heading (C to E) the taxa to which the symbols that are placed in those columns refer.

For example, if column C contains a symbol, the Remarks Column will give a list of those strongly differentiated subspecies meant by the symbol in C. If Column D contains a symbol, the Remarks Column will give a list of the other allospecies of this superspecies. If Column E contains a symbol the Remarks Column will give a list of the other species of the species group.

Since each taxon of the species category is counted only once, certain symbols for superspecies or allospecies, respectively, are placed in square brackets, as follows: if the superspecies is represented in North America by only a single allospecies, as in *Podiceps* [nigricollis], the symbol for the superspecies is bracketed. If a superspecies is represented in North America by two or more allospecies, as in *Gavia* [arctica], the symbols for the allospecies are bracketed.

The analytical table (Table 1) includes only those species that breed regularly in North America. Excluded are the Caribbean area (including the Bahamas), Mexico (including Baja California), and Greenland. All naturally occurring species, even spontaneous colonists like the Cattle Egret, that breed or once bred (recently extinct birds) are included, but species introduced by man are excluded. Strictly marine species breeding in North America are tabulated separately in the appendix to Table 1.

The units analyzed are two in number, the biological species and the zoogeographical species. The biological species, which in ornithology coincides with the taxonomic species, is used in the analysis of polytypic species. There are approximately 607 biological species in North America, applying the geographical limits set above. For the analysis of the superspecies, the zoogeographical species, our basic unit, is employed. As discussed above, zoogeographical species include both superspecies (comprised of two or more biological species, but counted as one zoogeographical species) and individual biological species not forming part of a superspecies. There are approximately 517 zoogeographical species in North America. This category of species is important in zoogeographical and ecological studies, as was pointed out first by Rensch (1929). For instance, in studies of species diversity of different regions it is usually misleading to count parapatric species separately when they are members of the same superspecies.

The sequence of families exactly follows the A.O.U. Check-list, except that strictly marine families (e.g. Alcidae) and species are listed separately in an appendix to Table 1. These are species breeding near the sea and foraging entirely in the ocean or at the edges. It seemed important to treat these as a separate group for comparison of species structure with land and fresh-water groups.

The families are somewhat arbitrarily designated by double letters (from AA to HE). Zoogeographic species within each family are numbered consecutively such that each zoogeographic species has a distinctive letter-number combination, e.g., AA 1, HE 5, etc. This system of iden-

tification is helpful in tabulating and analyzing our results. The families are arranged in nine groups, identified by the first letter of the double letter combination (the second letter actually designates a particular family within the group indicated by the first letter). A rough summary of these groups is as follows (see Table 1 for details):

A — waterbirds

B — hawks, gallinaceous birds

C — rails, cranes, shorebirds, gulls

D — pigeons, parrots, cuckoos

E — owls, hummingbirds, woodpeckers

F — tyrant flycatchers

G — larks, swallows, crows, Old World oscines

H — nine-primaried oscines

Marine species

#### TABLE 1

## ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

A. monotypic species

B. uncomplicated polytypic species

C. strongly differentiated polytypic species

D. member of superspecies E. member of species group

| FAMILY, GENUS, SPECIES                                                                                                                            | A                        | В          | С  | D       | Е | REMARKS                                  |
|---------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|------------|----|---------|---|------------------------------------------|
| AA GAVIIDAE  1. Gavia [immer] G. [immer] immer G. [immer] adamsii 2. Gavia [arctica] G. [arctica] arctica G. [arctica] pacifica 3. Gavia stellata | [X]<br>[X]<br>[X]<br>[X] | [O]<br>O   | X  | х<br>—х |   |                                          |
| AB PODICIPEDIDAE  1. Podiceps grisegena 2. Podiceps auritus 3. Podiceps [nigricollis]                                                             | X<br>X                   | О          | [O | -O]     | 0 | D-andinus<br>E-occipitalis, taczanowskii |
| P. [nigricollis]                                                                                                                                  | X                        | О          |    |         |   | B-occipitans, taczanowskii               |
| nigricollis 4. Podiceps dominicus 5. Aechmophorus occidentalis                                                                                    | X<br>Xe                  | О          |    |         |   |                                          |
| 6. Podilymbus [podiceps] P. [podiceps] podiceps                                                                                                   | Ae                       | X          |    | [O]     |   | D-gigas                                  |
| AC PELECANIDAE 1. Pelecanus erythrorhynchos                                                                                                       | Xe                       |            |    |         |   |                                          |
| AD PHALACROCORACIDAE  1. Phalacrocorax [olivaceus] P. [olivaceus] olivaceus P. [olivaceus] auritus                                                | [X]                      | [O]<br>[X] |    | X       | 0 | E-aristotelis                            |

| FAMILY, GENUS, SPECIES                                                                               | A             | В           | С        | D   | Е        | REMARKS                                                               |
|------------------------------------------------------------------------------------------------------|---------------|-------------|----------|-----|----------|-----------------------------------------------------------------------|
| AE ANHINGIDAE<br>1. Anhinga [anhinga]                                                                |               |             |          | [O] |          | D-melanogaster, rufa,                                                 |
| A. [anhinga] anhinga                                                                                 | X             | Ο           |          |     |          | novaehollandiae                                                       |
| AF ARDEIDAE  1. Botaurus [stellatus]                                                                 |               |             |          | [O— | —O]      | D-lentiginosus, pinnatus, poeciloptilus                               |
| B. [stellatus] lentiginosus 2. Ixobrychus [minutus] I. [minutus] exilis                              | Xe            | X           | 0        | [O] |          | D-sinensis, exilis<br>C-erythromelas                                  |
| 3. Nycticorax [nycticorax] N. [nycticorax] nycticorax 4. Nycticorax violaceus                        | X<br>X        | 0           |          | [O] |          | D-caledonicus                                                         |
| <ul><li>5. Butorides [virescens]</li><li>B. [virescens] virescens</li><li>6. Bubulcus ibis</li></ul> | X             | X<br>O      | [O       | —O] |          | D-striatus                                                            |
| 7. Egretta caerulea<br>8. Egretta rufescens<br>9. Egretta tricolor                                   | X<br>X        | O<br>X<br>O |          |     |          |                                                                       |
| 10. Egretta [garzetta]<br>E. [garzetta] thula<br>11. Egretta alba                                    | X             | X<br>O      |          | [O] |          | D-thula, dimorpha                                                     |
| 12. Ardea [cinerea] A. [cinerea] cinerea                                                             |               |             | X<br>[O— | —O] |          | D-cocoi, melanocephala, pacifica? C-herodias, cinerea, "occidentalis" |
| AG CICONIIDAE  1. Mycteria americana                                                                 | X             |             |          |     |          | Polymorphic.                                                          |
| AH THRESKIORNITHIDAE                                                                                 | $\Lambda$     |             |          |     |          |                                                                       |
| <ol> <li>Plegadis [falcinellus]</li> <li>P. [falcinellus]</li> <li>falcinellus</li> </ol>            | [X]           |             |          | X   | 0        | E-ridgwayi                                                            |
| P. [falcinellus] chihi 2. Eudocimus albus 3. Platalea ajaja                                          | [X]<br>X<br>X |             |          | O—  | <u> </u> | E-ruber                                                               |
| AI ANATIDAE  1. Dendrocygna [bicolor]                                                                |               |             |          | [O] | 0        | D-arcuata                                                             |
| D. [bicolor] bicolor  2. Dendrocygna autumnalis  3. Cygnus cygnus                                    | X<br>X<br>X   | 0           | 0        | —О  | X        | E-javanica<br>C-buccinator                                            |
| 4. Cygnus columbianus                                                                                | X             |             | 0-       | _O  | X        | E-columbianus<br>C-bewickii                                           |
| 5. Anser fabalis                                                                                     | X             |             | 0        |     | X        | E-cygnus<br>C-brachyrhynchus, fabalis,                                |
|                                                                                                      |               |             |          |     |          | serrirostris groups E-erythropus, anser, albifrons                    |
| 6. Anser albifrons                                                                                   |               | X           | О        |     | X        | C-flavirostris E-erythropus, anser, fabalis                           |
| 7. Anser caerulescens                                                                                |               | X           |          |     | X        | Polymorphic<br>E-rossii                                               |
| 8. Anser rossii<br>9. Anser canagicus                                                                | Xe<br>X       |             |          |     | X        | E-caerulescens                                                        |
| 10. Branta canadensis                                                                                | A             |             | X        | _X  | X        | C-hutchinsii group<br>E-leucopsis                                     |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

D. member of superspecies E. member of species group

| FAMILY, GENUS, SPECIES                                                                                                                                 | A                        | В      | С   | D         | E                | REMARKS                                                                                                  |
|--------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|--------|-----|-----------|------------------|----------------------------------------------------------------------------------------------------------|
| <ul><li>11. Branta leucopsis</li><li>12. Branta bernicla</li><li>13. Aix sponsa</li><li>14. Anas [penelope]</li></ul>                                  | X<br>Xe                  |        | X—  | —х<br>[О] | X<br>O<br>O      | E-canadensis<br>C-nigricans<br>E-galericulata<br>D-americana<br>E-sibilatrix                             |
| A. [penelope] americana<br>15. Anas strepera<br>16. Anas crecca                                                                                        | Xe<br>X                  | Ο      | x-  | —X        | O                | C-carolinensis E-flavirostris, capensis,                                                                 |
| 17. Anas [platyrhynchos]                                                                                                                               |                          |        |     | X         | О                | formosa<br>E-melleri, poecilorhyncha,<br>undulata, luzonica                                              |
| A. [platyrhynchos] platyrhynchos A. [platyrhynchos] rubripes                                                                                           | [Xe]                     |        | [X] |           |                  | C-diazi, fulvigula, wyvilliana, laysanensis                                                              |
| 18. Anas [acuta]                                                                                                                                       |                          |        |     | [O]       | О                | D-georgica<br>E-bahamensis,                                                                              |
| A. [acuta] acuta<br>19. Anas discors<br>20. Anas cyanoptera<br>21. Anas clypeata                                                                       | X<br>Xe<br>X<br>X        | Ο      | О   |           | X<br>X<br>O?     | erythrorhyncha C-eatoni, drygalskii E-querquedula, cyanoptera E-discors, querquedula E-platalea, smithi, |
| 22. Aythya [ferina]                                                                                                                                    |                          |        |     | [O]       | X                | rhynchotis<br>D-valisineria<br>E-americana                                                               |
| A. [ferina] valisineria 23. Aythya americana 24. Aythya collaris 25. Aythya marila 26. Aythya affinis 27. Somateria mollissima                         | Xe<br>Xe<br>Xe<br>X<br>X | О      | X   | ?—<br>?—  | X<br>X<br>X<br>X | E-[ferina]  E-affinis E-marila C-mollissima, v-nigra groups                                              |
| 28. Somateria spectabilis 29. Somateria fischeri 30. Polysticta stelleri                                                                               | X<br>X<br>X              |        |     |           | X                | E-spectabilis<br>E-mollissima                                                                            |
| 31. Camptorhynchus labradorius 32. Histrionicus histrionicus 33. Clangula hyemalis 34. Melanitta nigra 35. Melanitta perspicillata 36. Melanitta fusca | Xe<br>X<br>X<br>X<br>Xe  | O<br>X | 0   |           |                  | Extinct  C-deglandi                                                                                      |
| 37. Bucephala albeola 38. Bucephala islandica 39. Bucephala clangula 40. Mergus cucullatus 41. Mergus serrator                                         | Xe<br>X<br>X<br>Xe<br>X  | O<br>O |     |           | X<br>X<br>O<br>X | E-clangula E-islandica E-albellus E-merganser, squamatus, australis                                      |

| FAMILY, GENUS, SPECIES                                                                   | A           | В          | С   | D         | Е      | REMARKS                                                 |
|------------------------------------------------------------------------------------------|-------------|------------|-----|-----------|--------|---------------------------------------------------------|
| 42. Mergus merganser                                                                     | X           | O          |     |           | X      | E-serrator, squamatus, australis                        |
| 43. Oxyura dominica<br>44. Oxyura jamaicensis                                            | X<br>X      |            | О   | О—        | —О     | C-ferruginea<br>E-vittata, leucocephala,                |
| BA CATHARTIDAE  1. Cathartes aura  2. Coragyps atratus  3. Vultur californianus          | X<br>Xe     | X          |     |           |        | maccoa, australis                                       |
| BB ACCIPITRIDAE  1. Elanus [caeruleus]  E. [caeruleus] leucurus  2. Elanoides forficatus | X<br>X      | 0          | [O— | - O -     | —O]    | D-leucurus, notatus                                     |
| 3. Ictinia [plumbea] I. [plumbea] misisippiensis                                         | Xe          |            | [O— | —O]       |        | D-misisippiensis                                        |
| 4. Rostrhamus sociabilis 5. Accipiter [gentilis]                                         | X           | Ο          | [O— | —O]       | Ο      | E-hamatus<br>D-melanoleucus,<br>meyerianus, henstii?    |
| A. [gentilis] gentilis 6. Accipiter [nisus]                                              |             | X          |     | [O]       |        | D-striatus, madagascariensis,                           |
| A. [nisus] striatus                                                                      |             | X          | О   |           |        | rufiventris<br>C-chionogaster,<br>erythrocnemius,       |
| 7. Accipiter [bicolor] A. [bicolor] cooperii                                             | X<br>X      | O          |     | [O]       |        | ventralis<br>D-cooperii, gundlachi                      |
| 8. Buteo nitidus 9. Buteo lineatus                                                       |             | X          |     |           | Ο      | E-ridgwayi, leucorrhous?                                |
| 10. Buteo platypterus 11. Buteo brachyurus 12. Buteo swainsoni 13. Buteo [albicaudatus]  | X<br>X<br>X | U          | О—  | _O<br>[O] | X<br>X | C-albigula E-[albicaudatus] D-polyosoma, poecilochrous, |
| B. [albicaudatus]<br>albicaudatus                                                        | X           | O          |     |           |        | galapagoensis<br>E-swainsoni                            |
| 14. Buteo albonotatus                                                                    | X           |            | [0] | —Ol       |        | Diamaiannia vontralia                                   |
| 15. Buteo [buteo]                                                                        |             |            | [O— | _0,       |        | D-jamaicensis, ventralis, oreophilus,                   |
| B. [buteo] jamaicensis<br>16. Buteo lagopus<br>17. Buteo regalis                         | X<br>Xe     | О          | X   |           |        | brachypterus<br>C-harlani                               |
| 18. Parabuteo unicinctus<br>19. Buteogallus                                              |             | X          |     | [O]       |        | D-anthracinus                                           |
| [aequinoctialis] B. [aequinoctialis]                                                     | X           |            | 0—  | ?         |        | C-subtilis                                              |
| anthracinus                                                                              | X           | O          |     |           | O      | E-audax                                                 |
| 20. Aquila chrysaetos 21. Haliaetus [albicilla]                                          |             |            | x—  | —x        | O      | E-audax                                                 |
| H. [albicilla] albicilla<br>H. [albicilla]                                               | [X]         | [O]<br>[X] |     |           |        |                                                         |
| leucocephalus 22. Circus [cyaneus] C. [cyaneus] cyaneus                                  | X           | 0—         | [O— | —О]       |        | D-cinereus                                              |
| BC PANDIONIDAE  1. Pandion haliaetus                                                     | x           | O          |     |           |        |                                                         |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

D. member of superspecies

E. member of species group

| FAMILY, GENUS, SPECIES                                                                                                                                                                                                                                                   | A | В                      | С                     | D                  | Е        | REMARKS                                                                                      |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---|------------------------|-----------------------|--------------------|----------|----------------------------------------------------------------------------------------------|
| BD FALCONIDAE  1. Polyborus plancus  2. Falco [rusticolus]                                                                                                                                                                                                               | X |                        | О—                    | _O<br>[O]          | X        | C-cheriway, lutosus<br>D-altaicus<br>E-biarmicus, jugger,                                    |
| F. [rusticolus] rusticolus 3. Falco mexicanus 4. Falco [peregrinus]                                                                                                                                                                                                      | X | X                      | [O—                   | - O -              | X<br>—O] | cherrug, mexicanus  E-biarmicus, jugger, cherrug, [rusticolus] D-kreyenborgi, fasciinucha    |
| F. [peregrinus] peregrinus 5. Falco femoralis 6. Falco columbarius 7. Falco [tinnunculus]                                                                                                                                                                                | X | X<br>O<br>X            | О                     | [O]                | O?       | deiroleucus C-pelegrinoides  E-chicquera D-sparverius, moluccensis, cenchroides, newtoni,    |
| F. [tinnunculus] sparverius                                                                                                                                                                                                                                              |   | X                      | O                     |                    |          | punctatus, araea E-naumanni, alopex, rupicoloides C-sparveroides, caribaearum                |
| BE CRACIDAE  1. Ortalis [vetula]                                                                                                                                                                                                                                         |   |                        | [O                    | - O -              | —O]      | D-ruficauda,                                                                                 |
| O. [vetula] vetula                                                                                                                                                                                                                                                       | X | О                      |                       |                    |          | poliocephala                                                                                 |
| BF "TETRAONIDAE"  1. Dendragapus obscurus  2. Dendragapus canadensis                                                                                                                                                                                                     |   |                        | Xe-                   | —Х <b>е</b><br>—Хе | 0        | C-obscurus, fuliginosus<br>groups<br>C-canadensis, franklinii                                |
| <ol> <li>Bonasa umbellus</li> <li>Lagopus lagopus</li> <li>Lagopus mutus</li> <li>Lagopus leucurus</li> <li>Tympanuchus cupido</li> <li>Tympanuchus         <ul> <li>phasianellus</li> </ul> </li> <li>Centrocercus         <ul> <li>urophasianus</li> </ul> </li> </ol> |   | Xe—X<br>Xe<br>Xe<br>Xe | -Xe?<br>O<br>X<br>Xe- | —Xe                | O        | groups E-falcipennis E-bonasia, sewerzowi C-scoticus C-evermanni, rupestris C-pallidicinctus |
| BG PHASIANIDAE 1. Colinus virginianus                                                                                                                                                                                                                                    |   |                        | X                     | O—                 | _о       | C-ridgwayi, nigrogularis?<br>E-leucopogon, cristatus                                         |
| <ul> <li>2. Callipepla squamata</li> <li>3. Callipepla [californica]</li> <li>C. [californica]</li> <li>californica</li> <li>C. [californica] gambelii</li> </ul>                                                                                                        |   | [X]                    |                       | X                  | X        | E-picta, douglasii                                                                           |

| FAMILY, GENUS, SPECIES                                                                                                                                                          | A                   | В               | С   | D       | Е      | REMARKS                                                                                             |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------|-----------------|-----|---------|--------|-----------------------------------------------------------------------------------------------------|
| <ul><li>4. Callipepla picta</li><li>5. Cyrtonyx [montezumae]</li><li>C. [montezumae]</li><li>montezumae</li></ul>                                                               | X                   | X<br>O          |     | [O]     | X      | E-[californica], douglasii<br>D-sallei, ocellatus                                                   |
| BH "MELEAGRIDIDAE"  1. Meleagris gallopavo                                                                                                                                      |                     | X               |     |         |        |                                                                                                     |
| CA GRUIDAE 1. Grus americana 2. Grus canadensis                                                                                                                                 | Xe                  | X               | —X  |         | O?     | E-japonensis                                                                                        |
| CB ARAMIDAE  1. Aramus guarauna                                                                                                                                                 | X                   | 0               |     |         |        |                                                                                                     |
| CC RALLIDAE  1. Rallus [longirostris] R. [longirostris] longirostris R. [longirostris] elegans 2. Rallus [aquaticus] R. [aquaticus] limicola 3. Porzana carolina 4. Coturnicops | [X]<br>X<br>Xe<br>X | [X]<br>[O]<br>O | [O] | [O]     | 0<br>0 | C-obsoletus group  D-limicola  E-porzana, fluminea?                                                 |
| noveboracensis<br>5. Laterallus jamaicensis                                                                                                                                     |                     | X               | O   | _o      | _0     | E-exquisita C-spilonotus                                                                            |
| <ul><li>6. Porphyrula martinica</li><li>7. Gallinula chloropus</li><li>8. Fulica [atra]</li></ul>                                                                               | X<br>X              | 0-              | —о  | [O]     | О      | C-galeata, garmani,<br>brachyptera<br>E-tenebrosa, angulata<br>D-americana, caribaea,<br>leucoptera |
| F. [atra] americana                                                                                                                                                             | X                   | О               |     |         |        |                                                                                                     |
| CD CHARADRIIDAE  1. Charadrius [hiaticula] C. [hiaticula] hiaticula C. [hiaticula] semipalmatus 2. Charadrius melodus 3. Charadrius [alexandrinus]                              | [X]<br>[Xe]         | [O]<br>Xe       | [O  | X<br>O] | 0      | E-placidus  D-marginatus, occidentalis                                                              |
| C. [alexandrinus]                                                                                                                                                               |                     | X               |     |         |        | ruficapillus                                                                                        |
| alexandrinus 4. Charadrius wilsonia 5. Charadrius vociferus 6. Charadrius montanus 7. Eudromias morinellus 8. Pluvialis dominica 9. Pluvialis squatarola                        | X<br>Xe<br>X        | X<br>O<br>X     |     | O       | O<br>O | E-veredus, asiaticus<br>E-apricaria                                                                 |
| CE SCOLOPACIDAE  1. Arenaria [interpres]  A. [interpres] interpres  A. [interpres]  melanocephala  2. Scolopax minor  3. Gallinago gallinago                                    | [Xe]<br>Xe<br>X     | [X]             | 0—  | X<br>O  | 0      | E-rusticola, mira<br>C-nigripennis,                                                                 |
| 4. Numenius [arquata] N. [arquata] americanus 5. Numenius phaeopus                                                                                                              | X                   | Xe<br>O         |     | [O]     | X      | paraguaiae D-americanus E-tahitiensis, tenuirostris                                                 |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

D. member of superspecies E. member of species group

| FAMILY, GENUS, SPECIES                                                                                                                                                  | Α                             | В        | С   | D               | E      | REMARKS                                       |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|----------|-----|-----------------|--------|-----------------------------------------------|
| <ul> <li>6. Numenius tahitiensis</li> <li>7. Numenius [borealis]</li> <li>N. [borealis] borealis</li> <li>8. Bartramia longicauda</li> <li>9. Catoptrophorus</li> </ul> | Xe<br>Xe<br>Xe                | X        |     | [O]             | X      | E-phaeopus, tenuirostris<br>D-minutus         |
| semipalmatus 10. Tringa [incana] T. [incana] incana 11. Tringa hypoleucos 12. Tringa [ochropus]                                                                         | X<br>X                        |          | О—  | [O]<br>O<br>[O] | О      | D-brevipes C-macularia D-solitaria E-glareola |
| T. [ochropus] solitaria 13. Tringa [nebularia] T. [nebularia] melanoleuca 14. Tringa flavipes 15. Limosa fedoa                                                          | Xe<br>Xe<br>Xe                | Xe       |     | [O]             |        | D-melanoleuca                                 |
| <ul> <li>16. Limosa lapponica</li> <li>17. Limosa [limosa]</li> <li>L. [limosa] haemastica</li> <li>18. Limnodromus [griseus]</li> </ul>                                | X<br>Xe                       | 0        | X   | [O]<br>—X       | 0      | D-haemastica<br>E-semipalmatus                |
| L. [griseus] griseus L. [griseus] scolopaceus 19. Calidris canutus 20. Calidris [maritima] C. [maritima] maritima                                                       | [X]                           | [Xe]     | X   | —x              |        |                                               |
| C. [maritima] ptilocnemis 21. Calidris alpina 22. Calidris minutilla 23. Caldris bairdii 24. Calidris fuscicollis 25. Calidris melanotos                                | Xe<br>X<br>Xe<br>X            | [X]<br>X |     |                 | 0      | E-ferruginea, acuminata?,                     |
| 26. Calidris ruficollis 27. Calidris pusilla 28. Calidris mauri 29. Calidris alba 30. Micropalama himantopus 31. Tryngites subruficollis                                | X<br>Xe<br>X<br>X<br>Xe<br>Xe |          |     |                 | X<br>X | fuscicollis?  E-mauri E-pusilla               |
| 32. Aphriza virgata  CF RECURVIROSTRIDAE  1. Recurvirostra [avosetta]                                                                                                   | Xe                            |          | [O— | —O]             |        | D-americana, andina,<br>novaehollandiae       |
| R. [avosetta] americana 2. Himantopus [himantopus] H. [himantopus] mexicanus                                                                                            | Xe<br>X                       |          | [O— | —O]             |        | D-8 "species," see text.                      |

| FAMILY, GENUS, SPECIES                                                                               | A             | В      | С       | D        | Е              | REMARKS                                                                                        |
|------------------------------------------------------------------------------------------------------|---------------|--------|---------|----------|----------------|------------------------------------------------------------------------------------------------|
| CG PHALAROPODIDAE  1. Phalaropus fulicarius 2. Phalaropus lobatus 3. Phalaropus tricolor             | X<br>X<br>Xe  |        |         |          |                |                                                                                                |
| CH STERCORARIIDAE  1. Stercorarius pomarinus 2. Stercorarius parasiticus 3. Stercorarius longicaudus | X<br>X<br>X   |        |         |          |                |                                                                                                |
| CI LARIDAE 1. Larus atricilla 2. Larus pipixcan 3. Larus philadelphia                                | X<br>Xe<br>Xe |        |         | о—       | _о             | E-ridibundus,<br>brunneicephalus,                                                              |
| <ul><li>4. Larus sabini</li><li>5. Larus delawarensis</li><li>6. Larus canus</li></ul>               | X<br>Xe<br>X  | O      |         | ?—<br>?— | O?<br>—X<br>—X | serranus, maculipennis E-furcatus E-canus, kamtschatschensis E-delawarensis, kamtschatschensis |
| 7. Larus hyperboreus                                                                                 | 1             | X      |         |          | X              | E-CI 8-12, and fuscus, schistisagus,                                                           |
| 8. Larus californicus                                                                                | Xe            |        |         |          | X              | occidentalis E-CI 7, 9-12, and fuscus, schistisagus,                                           |
| 9. Larus glaucescens                                                                                 | X             |        |         | ?—       | _X             | occidentalis E-CI 7-8, 10-12, and fuscus, schistisagus,                                        |
| 10. Larus argentatus                                                                                 | X             |        | 0       | ?—       | —х             | occidentalis<br>C-cachinnans<br>E-CI 7-9, 11-12, and<br>fuscus, schistisagus,                  |
| 11. Larus thayeri                                                                                    | Xe            |        |         | ?—       | —X             | occidentalis E-CI 7-10, 12, and fuscus, schistisagus,                                          |
| 12. Larus glaucoides                                                                                 |               | X      |         | ?—       | —X             | occidentalis E-CI 7-11, and fuscus, schistisagus,                                              |
| 13. Larus [marinus] L. [marinus] marinus                                                             | x             |        | [O      | —O]      |                | occidentalis<br>D-dominicanus                                                                  |
| 14. Rynchops nigra<br>15. Sterna nilotica                                                            | X             | O<br>X |         | O—       | —О             | E-flavirostris, albicollis                                                                     |
| 16. Sterna caspia<br>17. Sterna hirundo                                                              | X<br>X        |        | 0       |          | X              | C-longipennis<br>E-paradisaea, vittata,                                                        |
| 18. Sterna paradisaea                                                                                | X             |        |         | ?—       | —X             | virgata, hirundinacea D-vittata? E-hirundo, virgata, hirundinacea, vittata                     |
| <ul><li>19. Sterna forsteri</li><li>20. Sterna [albifrons]</li></ul>                                 | Xe            |        | [O      | - O -    | —O]            | D-lorata, nereis,                                                                              |
| S. [albifrons] albifrons<br>21. Chlidonias niger                                                     | X             | X<br>O |         |          | O              | superciliaris<br>E-hybrida, leucoptera                                                         |
| DA COLUMBIDAE  1. Columba leucocephala  2. Columba [fasciata]  C. [fasciata] fasciata                | X             | X      | [O<br>O | O]       | Ο              | E-speciosa, squamosa<br>D-araucana, caribaea<br>C-albilinea                                    |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

D. member of superspecies E. member of species group

| FAMILY, GENUS, SPECIES                                                                                                                                                                                           | Α                 | В                | С          | D.              | Е   | REMARKS                                                                             |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------|------------------|------------|-----------------|-----|-------------------------------------------------------------------------------------|
| 3. Columba [inornata] C. [inornata] flavirostris 4. Zenaida asiatica 5. Zenaida [macroura] Z. [macroura] macroura 6. Ectopistes migratorius 7. Columbina passerina 8. Columbina squammata 9. Leptotila verreauxi | X<br>Xe<br>X<br>X | O<br>X<br>X<br>X | [O         | [O]<br>O]       | O   | D-oenops, flavirostris  D-auriculata, graysoni  Extinct E-minuta C-inca C-decipiens |
| DB PSITTACIDAE 1. "Conuropsis" carolinensis                                                                                                                                                                      |                   | Xe               |            | :               |     | Extinct                                                                             |
| DC CUCULIDAE  1. Coccyzus minor  2. Coccyzus [americanus]     C. [americanus] americanus 3. Coccyzus     erythrophthalmus 4. Geococcyx californianus 5. Crotophaga ani 6. Crotophaga sulcirostris                | X<br>Xe<br>X<br>X | X<br>O           | O<br>[O    | ?—<br>—O<br>—O] | —О  | C-ferrugineus<br>E-melacoryphus<br>D-euleri                                         |
| EA TYTONIDAE<br>1. Tyto [alba]<br>T. [alba] alba                                                                                                                                                                 | X                 |                  | 0          | [O—             | ?]  | D-rosenbergii<br>C-glaucops-nigrescens<br>group                                     |
| EB STRIGIDAE<br>1. Otus asio                                                                                                                                                                                     |                   |                  | x-         | _x              | X   | C-asio, kennicottii,<br>cooperi, seductus<br>groups<br>E-trichopsis                 |
| <ul><li>2. Otus trichopsis</li><li>3. Otus [scops]</li></ul>                                                                                                                                                     | X                 | Ο                |            | [O]             | X   | E-asio, bakkamoena? D-flammeolus E-brucei                                           |
| O. [scops] flammeolus 4. Bubo [bubo] B. [bubo] virginianus 5. Nyctea scandiaca 6. Surnia ulula 7. Glaucidium [gnoma]                                                                                             | X<br>X<br>X       | O<br>X<br>O      | O          | [O—             | _O] | D-virginianus, africanus<br>C-nacurutu, nigrescens<br>D-siju<br>E-[brasilianum],    |
| G. [gnoma] gnoma                                                                                                                                                                                                 |                   | X                | <u> </u> ? |                 |     | minutissimum,<br>perlatum?                                                          |

| FAMILY, GENUS, SPECIES                                                                               | A             | В          | С   | D              | E   | REMARKS                                                    |
|------------------------------------------------------------------------------------------------------|---------------|------------|-----|----------------|-----|------------------------------------------------------------|
| 8. Glaucidium [brasilianum]                                                                          |               |            | [O— | —O]            | X   | D-nanum, jardinii<br>E-[gnoma], minutissimum,<br>perlatum? |
| G. [brasilianum]<br>brasilianum                                                                      | X             | Ο          |     |                |     | •                                                          |
| 9. Micrathene whitneyi 10. Athene cunicularia                                                        |               | X<br>X     | 0   |                | О   | C-graysoni<br>C-nanodes, cunicularia<br>brachyptera        |
| <ul><li>11. Strix [varia]</li><li>S. [varia] varia</li><li>S. [varia] occidentalis</li></ul>         |               | [X]<br>[X] | [O] | X              | О   | E-noctua<br>E-uralensis, aluco<br>C-fulvescens             |
| 12. Strix nebulosa<br>13. Asio otus                                                                  | X             | O<br>X     |     | О—             | —о  | E-abyssinicus, clamator, stygius,                          |
| <ul><li>14. Asio flammeus</li><li>15. Aegolius funereus</li><li>16. Aegolius [acadicus]</li></ul>    | X<br>X        | 0          | [O— | —O]            | 0   | madagascarensis<br>E-capensis<br>D-ridgwayi                |
| A. [acadicus] acadicus                                                                               |               | X          |     | O <sub>1</sub> |     | E-harrisii                                                 |
| EC CAPRIMULGIDAE  1. Caprimulgus [carolinensis] C. [carolinensis]                                    | Xe            |            |     | [O—            | —O] | D-rufus                                                    |
| carolinensis  2. Caprimulgus [vociferus]  C. [vociferus] vociferus  3. Phalaenoptilus nuttallii      | Ac            | X<br>X     |     | [O]            |     | D-noctitherus                                              |
| <ul><li>4. Nyctidromus albicollis</li><li>5. Chordeiles minor</li></ul>                              | X             | O          | x   | —х             | X   | C-vicinus, gundlachii<br>E-acutipennis                     |
| 6. Chordeiles acutipennis                                                                            |               | X          |     |                | X   | E-minor                                                    |
| ED APODIDAE  1. Cypseloides [niger]                                                                  | v             | 0          |     | [O]            |     | D-lemosi, D? rothschildi,<br>fumigatus                     |
| C. [niger] niger  2. Chaetura [pelagica]                                                             | X             | Ο          |     | X              |     | D-chapmani                                                 |
| <ul><li>C. [pelagica] pelagica</li><li>C. [pelagica] vauxi</li><li>3. Aeronautes saxatilis</li></ul> | [Xe]<br>[X]   | X          | [O] |                |     | C-aphanes                                                  |
| EE TROCHILIDAE  1. Archilochus [colubris] A. [colubris] colubris                                     | [Xe]          |            |     | X              | X   | E-costae                                                   |
| A. [colubris] alexandri  2. Archilochus costae  3. Archilochus anna                                  | [X]<br>X<br>X |            |     |                | X   | E-[colubris]                                               |
| <ul><li>4. Selasphorus platycercus</li><li>5. Selasphorus [rufus]</li><li>S. [rufus] rufus</li></ul> | X<br>[Xe]     | O [Vo]     |     | Xe             |     |                                                            |
| S. [rufus] sasin 6. Stellula calliope 7. Eugenes fulgens 8. Lampornis clemenciae                     | X<br>X        | [Xe]       | O   | —О             |     | C-spectabilis                                              |
| 9. Amazilia [rutila]                                                                                 |               | _X         | [O  | -OJ            | 0   | D-yucatanensis<br>E-tzacatl                                |
| A. [rutila] yucatanensis                                                                             | X             | U          | l   |                |     | - Lucati                                                   |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

D. member of superspecies

E. member of species group

| FAMILY, GENUS, SPECIES                                                                                          | A        | В           | С       | D         | Е      | REMARKS                                                |
|-----------------------------------------------------------------------------------------------------------------|----------|-------------|---------|-----------|--------|--------------------------------------------------------|
| <ul><li>10. Hylocharis [leucotis]</li><li>H. [leucotis] leucotis</li><li>11. Cynanthus latirostris</li></ul>    | XX       | 0           | 0       | [O]<br>O— | —О     | D-xantusii<br>C-doubledayi, lawrencei<br>E-sordidus    |
| EF TROGONIDAE  1. Trogon elegans                                                                                |          | X           |         | i         |        |                                                        |
| EG ALCEDINIDAE  1. Ceryle alcyon  2. Chloroceryle americana                                                     |          | Xe<br>X     |         |           | 0      | E-torquata<br>E-amazona                                |
| EH PICIDAE  1. Picoides [scalaris] P. [scalaris] scalaris                                                       |          | [X]         | [O]     | X         | X      | E-pubescens<br>C-eremicus, lucasanus,                  |
| P. [scalaris] nuttallii 2. Picoides pubescens 3. Picoides borealis 4. Picoides stricklandi 5. Picoides villosus | [X]<br>X | Xe<br>Xe    | O—<br>X | —О        | X      | parvus  E-[scalaris]  C-arizonae  C-maynardi, piger,   |
| <ul><li>6. Picoides albolarvatus</li><li>7. Picoides arcticus</li><li>8. Picoides tridactylus</li></ul>         | Xe       | Xe<br>X     | 0       |           | X<br>X | picoideus, extimus E-tridactylus C-funebris            |
| 9. Melanerpes formicivorus                                                                                      |          | X           | О       |           | X      | E-arcticus<br>C-flavigula<br>E-erythrocephalus         |
| <ul><li>10. Melanerpes</li><li>erythrocephalus</li><li>11. Melanerpes [carolinus]</li></ul>                     |          | Xe          |         | X         | X      | E-formicivorus  D-hoffmanni, superciliaris             |
| M. [carolinus] carolinus<br>M. [carolinus] aurifrons                                                            |          | [Xe]<br>[X] | [O]     |           |        | E-rubricapillus, pygmaeus<br>C-dubius, polygrammus,    |
| M. [carolinus] uropygialis 12. Melanerpes lewis                                                                 | Xe       | [X]         |         |           |        | santacruzi                                             |
| <ul><li>13. Sphyrapicus [varius]</li><li>S. [varius] varius</li><li>S. [varius] nuchalis</li></ul>              | [Xe]     | [Xe]        | Xe      | —Xe       | X      | E-thyroideus                                           |
| S. [varius] ruber 14. Sphyrapicus thyroideus 15. Colaptes auratus                                               |          | [Xe]<br>Xe  | X—      | _X        | X      | E-[varius] C-auratus, cafer, chrysoides, mexicanoides, |
| 16. Dryocopus pileatus                                                                                          |          | Xe-         | -Xe     | 0-        | _О     | chrysocaulosus<br>groups.<br>E-lineatus, schulzi       |

| FAMILY, GENUS, SPECIES                                                                                                                     | A            | В           | С         | D               | Е            | REMARKS                                                               |
|--------------------------------------------------------------------------------------------------------------------------------------------|--------------|-------------|-----------|-----------------|--------------|-----------------------------------------------------------------------|
| <ul><li>17. Campephilus [principalis]</li><li>C. [principalis]</li><li>principalis</li></ul>                                               | X            | Ο           |           | [O]             |              | D-imperialis                                                          |
| FA COTINGIDAE  1. Platypsaris [minor]                                                                                                      |              |             | [O—       | -O]             | O            | D-aglaiae, homochrous<br>E-niger, rufus                               |
| P. [minor] aglaiae                                                                                                                         |              | X           |           |                 |              | D-mger, rurus                                                         |
| FB TYRANNIDAE 1. Tyrannus tyrannus 2. Tyrannus dominicensis                                                                                | Xe<br>X      | O           |           | :               | O            | E-caudifasciatus,<br>cubensis                                         |
| 3. Tyrannus [melancholicus]                                                                                                                |              |             | X         | —x              | Ο            | E-niveigularis, albogularis                                           |
| T. [melancholicus] melancholicus                                                                                                           | [X]          |             | [O]       |                 |              | C-melancholicus,<br>chloronotus groups.                               |
| T. [melancholicus] couchii                                                                                                                 | [X]          |             | :         |                 |              | Cinoronotus groups.                                                   |
| 4. Tyrannus verticalis                                                                                                                     | x            |             |           |                 | X            | E-vociferans,<br>crassirostris                                        |
| <ul><li>5. Tyrannus vociferans</li><li>6. Tyrannus crassirostris</li><li>7. Tyrannus forficatus</li></ul>                                  | X<br>X<br>Xe | Ο           |           |                 | X<br>X       | E-verticalis, crassirostris<br>E-verticalis, vociferans               |
| 8. Pitangus sulphuratus 9. Myiodynastes luteiventris                                                                                       | X<br>X       | O<br>O      |           |                 | О            | E-maculatus<br>(sibling species)                                      |
| <ul><li>10. Myiarchus [crinitus]</li><li>M. [crinitus] crinitus</li><li>M. [crinitus] tyrannulus</li></ul>                                 | [Xe]         | [X]         | [O]       | X               |              | C-brachyurus                                                          |
| <ol> <li>Myiarchus [cinerascens]</li> <li>M [cinerascens]</li> </ol>                                                                       | x            | O           | [0]       | [O—             | —O]          | D-nuttingi                                                            |
| cinerascens 12. Myiarchus tuberculifer 13. Sayornis phoebe 14. Sayornis nigricans 15. Sayornis saya                                        | X<br>Xe<br>X | O<br>O<br>X |           |                 | X            | E-nigricans<br>E-phoebe                                               |
| <ul><li>16. Empidonax flaviventris</li><li>17. Empidonax virescens</li></ul>                                                               | Xe<br>Xe     |             |           |                 |              |                                                                       |
| 18. Empidonax [traillii]<br>E. [traillii] traillii                                                                                         | [Xe]         |             | Xe—       | —Xe             |              | Sibling species with                                                  |
| E. [traillii] alnorum                                                                                                                      | [Xe]         |             |           |                 |              | alnorum Sibling species with traillii                                 |
| <ol> <li>Empidonax [minimus]</li> <li>[minimus] minimus</li> </ol>                                                                         | [Xe]         |             |           | Xe              |              | Sibling species with hammondii                                        |
| E. [minimus] hammondii                                                                                                                     | [Xe]         |             |           |                 |              | Sibling species with minimus                                          |
| 20. Empidonax oberholseri                                                                                                                  | Xe           |             |           |                 |              | Sibling species with                                                  |
| 21. Empidonax wrightii                                                                                                                     | Xe           |             |           |                 |              | wrightii Sibling species with oberholseri                             |
| <ul><li>22. Empidonax difficilis</li><li>23. Empidonax fulvifrons</li><li>24. Contopus borealis</li><li>25. Contopus [fumigatus]</li></ul> | X<br>Xe      | X           | O—<br>[O— | _O<br>O_<br>_O] | —О<br>Х<br>Х | C-flavescens E-atriceps E-[fumigatus] D-pertinax, lugubris E-borealis |
| C. [fumigatus] pertinax                                                                                                                    | X            | 0           |           |                 |              | D porcains                                                            |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

D. member of superspecies

E. member of species group

| FAMILY, GENUS, SPECIES                                                                                                | A        | В           | С        | D   | Е      | REMARKS                                                                   |
|-----------------------------------------------------------------------------------------------------------------------|----------|-------------|----------|-----|--------|---------------------------------------------------------------------------|
| 26. Contopus [virens] C. [virens] virens                                                                              | [Xe]     |             | X—       | —X  |        | Sibling species with sordidulus                                           |
| C. [virens] sordidulus<br>27. Pyrocephalus rubinus                                                                    |          | [X]<br>X    | О        |     |        | Sibling species with virens C-nanus, saturatus, obscurus                  |
| 28. Camptostoma [obsoletum]<br>C. [obsoletum] imberbe                                                                 |          | X           |          | [O] |        | D-imberbe                                                                 |
| GA ALAUDIDAE  1. Eremophila [alpestris] E. [alpestris] alpestris                                                      |          | !           | [O—<br>X | -O] |        | D-bilopha<br>C-see text                                                   |
| GB HIRUNDINIDAE  1. Tachycineta thalassina  2. Tachycineta bicolor  3. Progne [subis]                                 | X<br>Xe  | Ο           | [O—      | —OI |        | D-chalybea, dominicensis                                                  |
| P. [subis] subis 4. Riparia riparia 5. Stelgidopteryx ruficollis                                                      | X        | X<br>O<br>X |          | o—  | —О     | modesta  E-congica, paludicola                                            |
| 6. Hirundo [rustica]                                                                                                  |          |             |          | [O] | О      | D-tahitica, angolensis,<br>lucida<br>E-aethiopica, albigularis,<br>smithi |
| H. [rustica] rustica                                                                                                  | X        |             | О        |     |        | C-savignii, tytleri, erythrogaster                                        |
| <ul><li>7. Petrochelidon [fulva]</li><li>P. [fulva] pyrrhonota</li><li>P. [fulva] fulva</li></ul>                     | [X]      | [X]         | [O]      | X   |        | C-rufocollaris group                                                      |
| GC CORVIDAE  1. Perisoreus [infaustus] P. [infaustus] canadensis                                                      |          |             | Xe       | [O] |        | D-canadensis, internigrans<br>C-canadensis, obscurus                      |
| <ul><li>2. Cyanocitta cristata</li><li>3. Cyanocitta stelleri</li></ul>                                               |          | Xe<br>X     | 0        |     | X<br>X | groups E-stelleri C-azteca, coronata E-cristata                           |
| 4. Aphelocoma coerulescens                                                                                            |          |             | X<br>    |     |        | C-coerulescens, californica, woodhousei groups                            |
| <ul><li>5. Aphelocoma ultramarina</li><li>6. Cyanocorax yncas</li><li>7. Pica [pica]</li><li>P. [pica] pica</li></ul> | X<br>[X] | [O]         | O<br>X—  | _X  |        | C-luxuosa<br>D-nuttalli                                                   |
| P. [pica] nuttalli<br>8. Corvus [corax]                                                                               | [Xe]     |             |          | [O] | X      | D-ruficollis<br>E-tropicus, cryptoleucus                                  |
| C. [corax] corax                                                                                                      |          | X           |          |     |        | L-tropicus, cryptoleucus                                                  |

| FAMILY, GENUS, SPECIES                                                                               | A        | В           | С   | D   | Е   | REMARKS                                                                                     |
|------------------------------------------------------------------------------------------------------|----------|-------------|-----|-----|-----|---------------------------------------------------------------------------------------------|
| 9. Corvus cryptoleucus<br>10. Corvus [brachyrhynchos]                                                | Xe       |             |     | [O] | X   | E-tropicus, [corax] D-nasicus, leucognaphalus? E-jamaicensis, leucognaphalus?, [ossifragus] |
| C. [brachyrhynchos]<br>brachyrhynchos                                                                |          |             | X—  | —X  |     | C-caurinus                                                                                  |
| 11. Corvus [ossifragus]                                                                              |          |             |     | [O] | Ο   | D-imparatus, palmarum<br>E-jamaicensis,<br>leucognaphalus,<br>[brachyrhynchos]              |
| C. [ossifragus] ossifragus<br>12. Gymnorhinus                                                        | Xe<br>Xe |             |     |     |     |                                                                                             |
| cyanocephalus<br>13. Nucifraga columbiana                                                            | Xe       |             |     |     | 0   | E-caryocatactes                                                                             |
| GD PARIDAE  1. Parus [atricapillus]                                                                  |          |             | х—  | X   | X   | D-sclateri?, montanus                                                                       |
| P. [atricapillus] atricapillus                                                                       |          | [Xe]        |     |     |     | E-gambeli, sclateri                                                                         |
| P. [atricapillus] carolinensis                                                                       |          | [Xe]        |     |     |     |                                                                                             |
| 2. Parus sclateri                                                                                    | X        | Ο           |     | ?—  | —X  | D-possibly with [atricapillus]                                                              |
| 3. Parus gambeli                                                                                     |          | X           |     |     | X   | E-[atricapillus], gambeli<br>E-sclateri, [atricapillus]                                     |
| 4. Parus [hudsonicus] P. [hudsonicus]                                                                |          | [Xe]        |     | X   |     |                                                                                             |
| hudsonicus P. [hudsonicus] cinctus P. [hudsonicus] rufescens                                         | [X]      | [O]<br>[Xe] |     |     | k   |                                                                                             |
| <ul><li>5. Parus wollweberi</li><li>6. Parus [bicolor]</li><li>P. [bicolor] bicolor</li></ul>        | X        | O           | (V) | X   | —X  | D-inornatus                                                                                 |
| <ul><li>P. [bicolor] bicolor</li><li>P. [bicolor] inornatus</li><li>7. Auriparus flaviceps</li></ul> |          | [X]<br>X    | [X] |     |     | C-atricristatus                                                                             |
| 8. Psaltriparus minimus                                                                              |          | 11          | X   |     |     | C-includes morph<br>melanotis; also<br>plumbeus and<br>minimus groups                       |
| GE SITTIDAE  1. Sitta carolinensis                                                                   |          | X           |     | 10  | 01  | Dedicale willow                                                                             |
| <ul><li>2. Sitta [canadensis]</li><li>S. [canadensis] canadensis</li></ul>                           | Xe       |             |     | [O  | —O] | D-whiteheadi, villosa,<br>yunnanensis                                                       |
| 3. Sitta pusilla                                                                                     | AC       |             | X   | -X  |     | C-pygmaea                                                                                   |
| GF CERTHIIDAE  1. Certhia familiaris                                                                 |          | X           | О   |     |     | C-americana group                                                                           |
| GG "CHAMAEIDAE"  1. Chamaea fasciata                                                                 |          | X           |     |     |     |                                                                                             |
| GH "CINCLIDAE"  1. Cinclus mexicanus                                                                 | X        |             | О   |     |     | C-ardesiaca                                                                                 |

#### TABLE<sub>(</sub>1 (cont.)

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

D. member of superspecies E. member of species group

| FAMILY, GENUS, SPECIES                                                        | A        | В        | С  | D   | Е      | REMARKS                                                                               |
|-------------------------------------------------------------------------------|----------|----------|----|-----|--------|---------------------------------------------------------------------------------------|
| GI TROGLODYTIDAE  1. Troglodytes aedon                                        |          |          | x- | _X  | X      | C-brunneicollis, aedon,<br>musculus groups<br>E-solstitialis, rufulus,                |
| 2. Troglodytes troglodytes                                                    |          | X        | 0  |     | X      | troglodytes C-hirtensis, pallescens E-solstitialis, rufulus aedon                     |
| 3. Thryomanes [bewickii]<br>T. [bewickii] bewickii                            |          | X        | [O | -O] |        | D-sissonii                                                                            |
| 4. Thryothorus Iudovicianus                                                   |          | X        | 0  |     | О      | C-albinucha<br>E-[rufalbus], [leucotis],                                              |
| 5. Campylorhynchus<br>[brunneicapillus]                                       |          |          | [O | -O] | 0      | modestus, longirostris<br>D-yucatanensis, jocosus<br>E-gularis, rufinucha,<br>griseus |
| C. [brunneicapillus] brunneicapillus                                          |          | X        |    |     |        | griscus                                                                               |
| <ul><li>6. Cistothorus palustris</li><li>7. Cistothorus [platensis]</li></ul> |          | X        | [O | -O] | 0      | D-apolinari<br>E-meridae                                                              |
| C. [platensis] platensis                                                      | X        | X        | 0  |     |        | E-meridae<br>C-stellaris group                                                        |
| <ul><li>8. Salpinctes mexicanus</li><li>9. Salpinctes obsoletus</li></ul>     | X        | Λ        | 0  |     |        | C-guttatus, fasciatus                                                                 |
| GK MIMIDAE  1. Mimus polyglottos                                              | X        |          | O  | —О  | O      | C-magnirostris, gilvus<br>E-patagonicus, triurus                                      |
| 2. Toxostoma [rufum]<br>T. [rufum] rufum                                      |          | [Xe]     |    | X   |        | D-longirostre, guttatum                                                               |
| T. [rufum] longirostre 3. Toxostoma [cinereum] T. [cinereum] bendirei         | [X]<br>X | (O)<br>O | [O | -O] |        | D-bendirei                                                                            |
| 4. Toxostoma curvirostre 5. Toxostoma redivivum                               | Λ.       | X<br>X   | :  | ?   | O<br>X | E-ocellatum<br>D-dorsale?                                                             |
| 6. Toxostoma dorsale                                                          |          | X        |    | ?   | —X     | E-dorsale, lecontei D-redivivum?                                                      |
| 7. Toxostoma lecontei<br>8. Oreoscoptes montanus                              | Xe       | X        |    |     | X      | E-redivivum, lecontei<br>E-redivivum, dorsale                                         |
| 9. Dumetella carolinensis                                                     | Xe       |          |    | O   | —О     | E-glabrirostris                                                                       |
| GL TURDIDAE  1. Turdus migratorius  2. Zoothera naevia                        | ?        | X<br>—Xe | О  |     |        | C-confinis                                                                            |
| <ul><li>3. Hylocichla mustelina</li><li>4. Catharus guttatus</li></ul>        | Xe       | Xe       |    |     | X      | E-ustulatus, minimus,                                                                 |
| 5. Catharus ustulatus                                                         |          | Xe       |    |     | X      | fuscescens E-guttatus, minimus, fuscescens                                            |

| FAMILY, GENUS, SPECIES                                                                  | A       | В           | С   | D   | Е  | REMARKS                                                                          |
|-----------------------------------------------------------------------------------------|---------|-------------|-----|-----|----|----------------------------------------------------------------------------------|
| 6. Catharus minimus                                                                     |         | Xe          |     |     | X  | E-guttatus, ustulatus,                                                           |
| 7. Catharus fuscescens                                                                  |         | Xe          |     |     | X  | fuscescens E-guttatus, ustulatus, minimus                                        |
| 8. Sialia sialis<br>9. Sialia mexicana<br>10. Sialia currucoides                        | Xe      | X<br>X      |     |     |    | minings                                                                          |
| 11. Oenanthe oenanthe 12. Luscinia svecica                                              | X       | X           | 0   |     | i  | C-phillipsi, seebohmi<br>C-cyanecula, svecica                                    |
| 13. Myadestes townsendi                                                                 | X       | Ο           |     |     | 0  | groups E-obscurus, elisabeth, unicolor?                                          |
| GM SYLVIIDAE  1. Phylloscopus borealis 2. Regulus [regulus]                             | X       | 0           |     | [O] | O  | D-satrapa                                                                        |
| R. [regulus] satrapa 3. Regulus calendula 4. Polioptila caerulea 5. Polioptila melanura |         | X<br>X<br>X |     |     |    | E-ignicapillus, goodfellow                                                       |
| GN MOTACILLIDAE<br>1. Motacilla flava                                                   | X       |             | O—  | —О  |    | C-e.g., flava, feldegg,                                                          |
| 2. Anthus spinoletta                                                                    |         | X           | 0   |     |    | thunbergi<br>C-spinoletta, petrosus                                              |
| 3. Anthus [furcatus]                                                                    |         |             | [O  | —O] | Ο  | groups D-spragueii E-campestris, godlewskii,                                     |
| A. [furcatus] spragueii                                                                 | Xe      |             |     |     |    | berthelotii                                                                      |
| GO BOMBYCILLIDAE  1. Bombycilla garrulus  2. Bombycilla cedrorum                        | X<br>Xe | 0           |     |     |    |                                                                                  |
| GP PTILOGONATIDAE  1. Phainopepla nitens                                                |         | X           |     |     |    |                                                                                  |
| GQ LANIIDAE  1. Lanius [excubitor]                                                      |         |             | X   | —х  | 0  | D-sphenocercus,<br>ludovicianus                                                  |
| L [excubitor] excubitor                                                                 |         | [X]         | [O] |     |    | E-see text C-excubitor, meridionalis                                             |
| L. [excubitor] ludovicianus                                                             |         | [X]         |     |     |    | groups                                                                           |
| HA VIREONIDAE  1. Vireo huttoni                                                         | v       | X           |     |     | X  | E-atricapilla                                                                    |
| <ul><li>2. Vireo atricapilla</li><li>3. Vireo [griseus]</li></ul>                       | X       |             | [O  | —O] | XX | E-huttoni D-pallens E-bellii, vicinior, latimeri, bairdi, carmioli,              |
| V. [griseus] griseus                                                                    |         | X           | О   |     |    | nelsoni<br>C-crassirostris, modestus,                                            |
| 4. Vireo bellii                                                                         |         | X           |     |     | X  | caribaeus, gundlachii E-[griseus], vicinior, latimeri, bairdi, carmioli, nelsoni |

## ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

A. monotypic species

B. uncomplicated polytypic species

D. member of superspecies E. member of species group

C. strongly differentiated polytypic species

FAMILY, GENUS, SPECIES C D E REMARKS A  $\mathbf{B}$ Xe X 5. Vireo vicinior E-[griseus], bellii, latimeri, bairdi, carmioli, nelsoni \_\_? E-flavifrons 6. Vireo solitarius X-Xe -X 7. Vireo flavifrons E-solitarius  $\mathbf{X}$ E-hypochryseus, Xe 8. Vireo philadelphicus [olivaceus], gilvus  $\mathbf{X}$ 9. Vireo [olivaceus] X D-altiloquus E-philadelphicus, hypochryseus, gilvus [O--?] C-flavoviridis, chivi, V. [olivaceus] olivaceus [X]gracilirostris V. [olivaceus] altiloquus [O] X [X]10. Vireo gilvus O-0 X C-leucophrys E-philadelphicus, hypochryseus, [olivaceus] HB PARULIDAE 1. Mniotilta varia Xe 2. Vermivora bachmanii X Xe E-[pinus] E-bachmanii 3. Vermivora [pinus] Xe V. [pinus] pinus V. [pinus] chrysoptera [Xe][Xe] 4. Vermivora peregrina Xe 5. Vermivora celata X Χ E-[ruficapilla], luciae X 6. Vermivora [ruficapilla] Χ--X E-celata, luciae V. [ruficapilla] [Xe] ruficapilla V. [ruficapilla] virginiae [Xe]V. [ruficapilla] crissalis [X] X 7. Vermivora luciae X E-celata, [ruficapilla] 8. Parula americana X--X C-americana, pitiayumi, graysoni 9. Dendroica petechia X O-O. C-petechia, aestiva, erithachorides groups 10. Dendroica pensylvanica Xe 11. Dendroica cerulea Xe 12. Dendroica caerulescens Xe--? 13. Dendroica [dominica] X D-adelaidae, pityophila D. [dominica] dominica [X][X] X D. [dominica] graciae [O] 14. Dendroica nigrescens E-[virens], fusca X 15. Dendroica [virens] X E-nigrescens, fusca D. [virens] virens
D. [virens] occidentalis [Xe] C-chrysoparia [Xe] D. [virens] townsendi [Xe]16. Dendroica fusca Xe E-nigrescens, [virens] X 17. Dendroica pinus X E-[discolor], palmarum

| FAMILY, GENUS, SPECIES                                                                                                                       | Α                     | В                 | С   | D       | Е                 | REMARKS                                                                                                                    |
|----------------------------------------------------------------------------------------------------------------------------------------------|-----------------------|-------------------|-----|---------|-------------------|----------------------------------------------------------------------------------------------------------------------------|
| 18. Dendroica [discolor]                                                                                                                     |                       |                   |     | [O]     | X                 | D-vitellina<br>E-pinus, palmarum                                                                                           |
| D. [discolor] discolor<br>19. Dendroica palmarum<br>20. Dendroica tigrina<br>21. Dendroica magnolia<br>22. Dendroica coronata                | Xe<br>Xe              | Xe<br>Xe          | x—  | X       | X<br>X?<br>X<br>X | E-pinus, [discolor] E-magnolia, coronata E-tigrina?, coronata C-auduboni E-tigrina?, magnolia                              |
| <ul><li>23. Dendroica kirtlandii</li><li>24. Dendroica striata</li><li>25. Dendroica castanea</li><li>26. Setophaga ruticilla</li></ul>      | Xe<br>Xe<br>Xe<br>Xe— | ?                 |     |         | X<br>X            | E-castanea<br>E-striata                                                                                                    |
| 27. Seiurus aurocapillus 28. Seiurus noveboracensis 29. Seiurus motacilla 30. Helmitheros swainsonii 31. Helmitheros vermivorus              | Xe—<br>Xe<br>Xe<br>Xe | Xe<br>?           |     | ?—      | —X<br>—X          | E-motacilla<br>E-noveboracensis                                                                                            |
| 32. Protonotaria citrea 33. Geothlypis trichas                                                                                               | Xe                    | X                 | 0   |         | O                 | C-beldingi, flavovelata<br>chapalensis<br>E-nelsoni                                                                        |
| <ul><li>34. Geothlypis poliocephala</li><li>35. Oporornis formosus</li><li>36. Oporornis agilis</li><li>37. Oporornis philadelphia</li></ul> | X<br>Xe<br>Xe         | О                 | Xe- | —Xe     | X<br>X            | E-philadelphia<br>C-tolmiei                                                                                                |
| 38. Wilsonia citrina 39. Wilsonia pusilla 40. Wilsonia canadensis 41. Myioborus pictus 42. Peucedramus taeniatus 43. Icteria virens          | Xe<br>Xe<br>X<br>X    | Xe<br>O<br>O<br>X |     |         |                   | E-agilis                                                                                                                   |
| HC ICTERIDAE  1. Dolichonyx oryzivorus  2. Sturnella [magna]  S. [magna] magna                                                               | Xe                    | [X]               | [O] | x       |                   | C-meridionalis, paralios,<br>praticola                                                                                     |
| S. [magna] neglecta 3. Agelaius phoeniceus                                                                                                   | [X]                   | X                 | 0   |         | X                 | Sibling species with neglecta Sibling species with magna C-assimilis, gubernator, nelsoni, subniger E-humeralis, tricolor, |
| 4. Agelaius tricolor                                                                                                                         | Xe                    |                   |     |         | X                 | xanthomus E-phoeniceus, humeralis, xanthomus                                                                               |
| <ul><li>5. Xanthocephalus xanthocephalus</li><li>6. Quiscalus [mexicanus] Q. [mexicanus] mexicanus</li></ul>                                 | Xe                    | [X                | [O— | X<br>?] |                   | B-nelsoni, monsoni<br>C-palustris                                                                                          |
| Q. [mexicanus] major                                                                                                                         |                       | [Xe]              |     |         |                   | Sibling species with major<br>Sibling species with<br>mexicanus                                                            |
| 7. Quiscalus quiscula                                                                                                                        |                       |                   | Xe  | ?       | —О                | C-quiscula, versicolor<br>E- lugubris, niger,<br>nicaraguensis                                                             |
| <ul><li>8. Euphagus carolinus</li><li>9. Euphagus cyanocephalus</li><li>10. Molothrus aeneus</li></ul>                                       | Xe<br>Xe<br>X         | O                 |     |         | X<br>X            | E-cyanocephalus<br>E-carolinus                                                                                             |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6).

D. member of superspecies E. member of species group

| FAMILY, GENUS, SPECIES                                                                                                      | A           | В             | С   | D   | Е   | REMARKS                                            |
|-----------------------------------------------------------------------------------------------------------------------------|-------------|---------------|-----|-----|-----|----------------------------------------------------|
| <ul><li>11. Molothrus ater</li><li>12. Icterus gularis</li><li>13. Icterus cucullatus</li><li>14. Icterus galbula</li></ul> | X           | X<br>O<br>X   | X   | _X  | 0   | E-nigrogularis C-galbula, bullockii, abeillei      |
| 15. Icterus spurius<br>16. Icterus graduacauda<br>17. Icterus parisorum                                                     | X<br>X<br>X | О             | 0   |     |     | E-pustulatus<br>C-fuertesi                         |
| HD THRAUPIDAE  1. Piranga [olivacea]  P. [olivacea] olivacea  P. [olivacea] ludoviciana                                     | [Xe]        |               |     | Xe  | 0   | E-leucoptera                                       |
| 2. Piranga flava                                                                                                            |             | X             | 0-  | —О  | X   | C-flava, lutea, hepatica groups                    |
| 3. Piranga rubra                                                                                                            |             | X             |     | ?   | _x  | E-rubra<br>E-flava                                 |
| HE FRINGILLIDAE  1. Carpodacus [erythrinus]                                                                                 |             |               |     |     | X   | D-purpureus                                        |
| C. [erythrinus] purpureus                                                                                                   |             | X             |     | [O— | —O] | E-cassinii<br>Sibling species with<br>cassinii     |
| 2. Carpodacus cassinii                                                                                                      | X           | <del></del> ? |     |     | X   | E-[erythrinus]. Sibling species with               |
| <ul><li>3. Carpodacus mexicanus</li><li>4. Pinicola enucleator</li></ul>                                                    |             | X<br>X        | 0   |     |     | purpureus<br>C-amplus, macgregori                  |
| 5. Loxia curvirostra                                                                                                        |             | X             | 0   |     | Ο   | C-himalayensis, altaiensis, scotica, guillemardi   |
| 6. Loxia leucoptera<br>7. Carduelis [spinus]                                                                                | X           | Ο             |     | [O] |     | E-pityopsittacus D-pinus                           |
| C. [spinus] pinus  8. Carduelis tristis                                                                                     | X           | O<br>Xe       |     |     |     | D-pinus                                            |
| 9. Carduelis psaltria                                                                                                       |             | 110           | X   |     | Ο   | C-hesperophila, psaltria<br>E-xanthogaster         |
| 10. Carduelis lawrencei<br>11. Acanthis [flammea]                                                                           | X           | ,             | X   | —х  | О   | D-hornemanni                                       |
| A. [flammea] flammea                                                                                                        |             | [X]           |     |     |     | E-flavirostris Sibling species with                |
| A. [flammea] hornemanni                                                                                                     | ,           |               | [X] |     |     | hornemanni<br>C-exilipes<br>Sibling species with   |
| 12. Leucosticte [arctoa]<br>L. [arctoa] arctoa                                                                              |             |               | X   | [O] |     | flammea D-brandti C-atrata, australis, tephrocotis |

| FAMILY, GENUS, SPECIES                                                                                                                                                                                                                   | Α           | В                            | С        | D          | Е           | REMARKS                                                                                                                                   |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------|------------------------------|----------|------------|-------------|-------------------------------------------------------------------------------------------------------------------------------------------|
| 13. Coccothraustes vespertinus                                                                                                                                                                                                           |             | X                            |          |            | 0           | E-abeillei                                                                                                                                |
| <ul> <li>14. Spiza americana</li> <li>15. Cardinalis [cardinalis]</li> <li>C. [cardinalis] cardinalis</li> <li>16. Cardinalis sinuata</li> <li>17. Pheucticus [ludovicianus]</li> <li>P. [ludovicianus]</li> <li>ludovicianus</li> </ul> | Xe<br>[Xe]  | XX                           | X        | [O]<br>—X  |             | D-phoeniceus  D-melanocephalus                                                                                                            |
| P [ludovicianus] melanocephalus 18. Passerina caerulea 19. Passerina [cyanea]                                                                                                                                                            |             | [X]<br>X                     | X        | X          | X           | D-amoena<br>E-versicolor, ciris                                                                                                           |
| P [cyanea] cyanea P. [cyanea] amoena 20. Passerina versicolor 21. Passerina ciris 22. Sporophila torqueola                                                                                                                               | [Xe]<br>[X] | X<br>X                       | O        |            | X<br>X<br>O | E-[cyanea], ciris E-[cyanea], versicolor C-torqueola, morelleti, sharpei E-americana, aurita,                                             |
| <ul> <li>23. Arremonops [rufivirgata]</li> <li>A. [rufivirgata]</li> <li>rufivirgata</li> <li>24. Pipilo chlorurus</li> <li>25. Pipilo erythrophthalmus</li> </ul>                                                                       | X<br>Xe     |                              | O<br>X   | [O]        | X<br>X      | collaris D-tocuyensis C-superciliosa, rufivirgata groups E-erythrophthalmus C-alleni, maculatus, erythrophthalmus, socorroensis, and ocai |
| 26. Pipilo [fuscus] P. [fuscus] fuscus                                                                                                                                                                                                   |             |                              | [X]      | X          |             | groups E-chlorurus D-aberti, albicollis C-crissalis, mesoleucos groups                                                                    |
| P. [fuscus] aberti 27. Calamospiza melanocorys 28. Ammodramus sandwichensis                                                                                                                                                              | Xe          | [X]                          | X        |            |             | C-princeps                                                                                                                                |
| 29. Ammodramus bairdii<br>30. Ammodramus savannarum                                                                                                                                                                                      | Xe          | X                            | О        |            |             | C-pratensis,                                                                                                                              |
| <ul><li>31. Ammodramus henslowii</li><li>32. Ammospiza leconteii</li><li>33. Ammospiza caudacuta</li><li>34. Ammospiza maritima</li></ul>                                                                                                | Xe          | Xe                           | Xe<br>Xe |            | X<br>X<br>X | E-caudacuta, maritima<br>C-nelsoni<br>E-leconteii, maritima<br>C-mirabilis, nigrescens                                                    |
| 35. Pooecetes gramineus 36. Chondestes grammacus 37. Aimophila carpalis 38. Aimophila ruficeps 39. Aimophila aestivalis 40. Aimophila botterii                                                                                           | X           | Xe<br>X<br>O<br>X<br>Xe<br>X | O        | <b>—</b> О | X<br>X      | E-caudacuta, leconteii  E-botterii, cassinii C-petenica                                                                                   |
| 41. Aimophila cassinii<br>42. Aimophila bilineata<br>43. Aimophila belli                                                                                                                                                                 | X           | X                            | X        |            | X<br>X<br>X | E-aestivalis, cassinii E-botterii, aestivalis E-belli C-belli, nevadensis groups                                                          |
| 44. Spizella arborea<br>45. Spizella passerina                                                                                                                                                                                           |             | Xe<br>X                      |          |            | x           | E-bilineata<br>E-breweri, pallida                                                                                                         |

#### ANALYTICAL TABLE OF SPECIES-LEVEL TAXA BREEDING IN NORTH AMERICA

(For explanation of symbols, etc., see pages 4-6)

A. monotypic species

D. member of superspecies E. member of species group

B. uncomplicated polytypic species
C. strongly differentiated polytypic species

| FAMILY, GENUS, SPECIES                                | A         | В        | С   | D  | Е  | REMARKS                                      |
|-------------------------------------------------------|-----------|----------|-----|----|----|----------------------------------------------|
| 46. Spizella pallida                                  | Xe        |          |     | ?— | —X | D-breweri?<br>E-breweri, passerina           |
| 47. Spizella breweri                                  |           | Xe       |     | ?— | X  | D-pallida?<br>E-pallida, passerina           |
| 48. Spizella pusilla<br>49. Spizella atrogularis      |           | Xe<br>X  |     | ?— | —О | E-wortheni                                   |
| 50. Passerella lincolnii<br>51. Passerella georgiana  |           | Xe<br>Xe |     | !  | X  | E-georgiana<br>E-lincolnii                   |
| 52. Passerella iliaca                                 |           | 110      | Xe  |    | 1  | C-unalaschcensis,<br>insularis               |
| 53. Passerella melodia                                | N.        |          | X   |    |    | C-see text                                   |
| 54. Zonotrichia querula<br>55. Zonotrichia leucophrys | Xe        |          | Xe  |    | X  | C-gambelii, leucophrys,                      |
|                                                       |           |          |     |    |    | nuttalli<br>E-[atricapilla]                  |
| 56. Zonotrichia<br>[atricapilla]                      |           |          |     | X  | X  | D-albicollis<br>E-leucophrys                 |
| Z. [atricapilla]<br>albicollis                        | [Xe]      |          |     |    |    |                                              |
| Z. [atricapilla]<br>atricapilla                       | [Xe]      |          |     |    |    |                                              |
| 57. Junco [hyemalis]<br>J. [hyemalis] hyemalis        |           |          | [X] | X  |    | D-phaeonotus, vulcani<br>C-hyemalis, aikeni, |
| <i>y</i> : [, e                                       |           |          | [,  |    |    | oreganus, caniceps, insularis                |
| J. [hyemalis] phaeonotus<br>58. Calcarius mccownii    | [X]<br>Xe |          | [O] |    |    | C-alticola, bairdi                           |
| 59. Calcarius lapponicus                              | Xe        | X        |     |    |    |                                              |
| 60. Calcarius ornatus 61. Calcarius pictus            | Xe        |          | 37  |    |    | C harrach areas                              |
| 62. Plectrophenax nivalis                             | 1         | I        | X   | İ  | l  | C-hyperboreus                                |

#### TABLE 1 (APPENDIX)

#### MARINE SPECIES

| FAMILY, GENUS, SPECIES                                                                                                                   | A | В | <u>C /</u>     | D   | <u>E</u> | REMARKS                                       |
|------------------------------------------------------------------------------------------------------------------------------------------|---|---|----------------|-----|----------|-----------------------------------------------|
| <ol> <li>Fulmarus [glacialis]</li> <li>F. [glacialis] glacialis</li> <li>Oceanodroma furcata</li> <li>Oceanodroma [leucorhoa]</li> </ol> | X | X |                | [O] | v        | D-glacialoides                                |
| O. [leucorhoa] leucorhoa 4. Oceanodroma homochroa 5. Pelecanus occidentalis                                                              | X | X | O <sub>.</sub> | [O] | X        | D-castro E-homochroa C-monorhis E-[leucorhoa] |

| MILY, GENUS, SPECIES                                                                                                                                                           | A                     | В                | С  | D         | Е      | REMARKS                                                                |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------|------------------|----|-----------|--------|------------------------------------------------------------------------|
| 6. Sula bassana 7. Phalacrocorax carbo 8. Phalacrocorax penicillatus 9. Phalacrocorax pelagicus 10. Phalacrocorax urile 11. Haematopus [ostralegus]                            | X<br>X<br>X           | O<br>X           | 0  | [O]       | X<br>X | C-capensis  E-urile E-pelagicus D-leucopodus,                          |
| H. [ostralegus]<br>ostralegus<br>12. Larus tridactylus<br>13. Larus brevirostris                                                                                               | X                     | X                | X  |           | X<br>X | fuliginosus C-moquini, bachmani, unicolor E-brevirostris E-tridactylus |
| <ul> <li>14. Larus eburneus</li> <li>15. Larus occidentalis</li> <li>16. Sterna [maxima]</li> <li>S. [maxima] maxima</li> <li>17. Sterna [sandvicensis]</li> </ul>             | X                     | Xe<br>O          |    | [O]       | X      | E-argentatus group, 8 sp. D-bergii D-elegans, zimmermanni,             |
| S. [sandvicensis] sandvicensis 18. Sterna dougallii                                                                                                                            | X<br>X                | 0                |    | [0]       | 0      | bengalensis  E-sumatrana                                               |
| <ul><li>19. Sterna aleutica</li><li>20. Sterna [fuscata]</li><li>S. [fuscata] fuscata</li><li>21. Pinguinus impennis</li></ul>                                                 | Xe<br>X<br>X          | 0                |    | [O]       |        | D-anaethetus, lunata  Extinct                                          |
| <ul><li>22. Alca torda</li><li>23. Uria aalge</li><li>24. Uria lomvia</li><li>25. Plautus alle</li></ul>                                                                       | X                     | O<br>X<br>X<br>O | 77 | 7.        |        |                                                                        |
| 26. Cepphus [grylle] C. [grylle] grylle C. [grylle] columba 27. Brachyramphus [hypoleucus]                                                                                     |                       | [X]<br>[X]       | X  | —X<br>—OI |        | D-carbo D-craveri                                                      |
| B. [hypoleucus] hypoleucus 28. Brachyramphus brevirostris                                                                                                                      | Xe<br>Xe              | 0                |    |           |        |                                                                        |
| 29. Brachyramphus<br>marmoratus<br>30. Synthliboramphus<br>antiquus                                                                                                            | X                     | O                | 0- | -О        |        | C-wumizusume                                                           |
| <ul> <li>31. Ptychoramphus aleuticus</li> <li>32. Aethia cristatella</li> <li>33. Aethia pusilla</li> <li>34. Aethia pygmaea</li> <li>35. Cyclorrhynchus psittacula</li> </ul> | X<br>X<br>X<br>X<br>X | O                |    |           |        |                                                                        |
| 36. Cerorhinca  monocerata  37. Fratercula [arctica]  F. [arctica] arctica  F. [arctica] corniculata  38. Lunda cirrhata                                                       | X [X]                 | [X]              |    | X         |        |                                                                        |

## III

## TAXONOMIC COMMENTS

The taxonomy of North American birds continues to be very active, and there have been steady improvements in their classification. The fact that many American taxonomists have applied their knowledge of Middle and South American birds, and of Eurasian birds, to the taxonomy of North American birds has been very beneficial. So has been the utilization of new behavorial, anatomical, physiological, and biochemical characters. As a result, the most recent A.O.U. Check-list (1957) is badly out of date, especially in the expression of the relationships of species in a meaningful sequence, in the indication of superspecies and species groups, and in the recognition of genera.

The vast literature that has accumulated in recent years is widely scattered (see literature cited) and as a result it is difficult for beginners, as well as for non-specialists, to find the relevant literature. One of the objects of these comments is to provide a convenient entry into the literature for such persons. Another objective is to explain the taxonomic decisions of necessity embodied in Table 1. In particular we have attempted to supply justification whenever we deviate from the published literature. If comments are lacking for a species, it indicates that no research has been conducted in recent years that has affected the generally accepted taxonomic position of that species.

Some readers who are not experienced in the traditions of taxonomy may find some of our conclusions too "subjective." They should remember that almost all conclusions in science are subjective. What is accepted by science at any given time is what appears to be the most valid inference from the currently available evidence. Changes occur when new facts become available or when there is a change in concepts. For instance, the change of the generic concept in ornithology in the last 50 years has necessitated many changes in successive editions of the A.O.U. Check-list. An experienced taxonomist has the privilege, perhaps one might even say the obligation, to suggest changes when he feels that previously adopted arrangements no longer represent the best current thinking or no longer reflect the most recently acquired information. From that point on, it will be the task of other specialists to weigh the soundness of the new suggestion and either to accept or reject it.

AA 1. Gavia [immer]. The component species (immer and adamsii) of this superspecies are largely allopatric, with some overlap (Rand, 1948; Godfrey, 1966), and are very similar in morphology and habits (Palmer, 1962).

AA 2. Gavia [arctica]. G. arctica and G. pacifica occupy continguously allopatric ranges, and come into contact (pacifica with G. arctica

viridigularis) in Anadyrland (Vaurie, 1965a) and in western Alaska (Gabrielson and Lincoln, 1959; Palmer, 1962). They occur sympatrically without interbreeding in at least some localities in Anadyrland. Only a few individuals of viridigularis occur in Alaska, and there are some indications that sporadic hybrids occur (Gabrielson and Lincoln, 1959). We tentatively consider them to comprise a superspecies. Palmer (1962) discussed variation in *G. arctica*.

- AA 3. Gavia stellata. This distinctive species is probably nearest to G. [arctica]. Johansen (1956) discussed its variation.
- AB 1. Podiceps grisegena. The races of this species are discussed in Palmer (1962).
- AB 2. Podiceps auritus. We consider this species monotypic, as the described races (Parkes, 1952b) are not sufficiently distinct to merit recognition.
- AB. 3. Podiceps [nigricollis]. P. andinus, a nearly extinct Andean form, is closely related to nigricollis, but probably not conspecific (Storer, pers. comm.; see also Vaurie, 1965a). These are considered to comprise a superspecies. P. occipitalis and P. taczanowskii of South America are closely related (Storer, 1963b) offshoots of the same stock that gave rise to andinus and nigricollis.
- AB 4. Podiceps dominicus. Races of this species are discussed in Palmer (1962). Its relationships are uncertain (Storer, 1963b).
- AB 5. Aechmophorus occidentalis. This species is apparently not a relative of "Podiceps" major (Wetmore and Parkes, 1954; Storer, 1963a). Color phases were described by Storer (1965). No races are recognized.
- AB 6. Podilymbus [podiceps]. The giant species gigas (Guatemala) is considered to comprise a superspecies with podiceps. Subspecies of podiceps are discussed in Palmer (1962).
- AC 1. Pelecanus erythrorhynchos. The monotypic North American White Pelican is probably not closely related to other (Old World) white pelicans.
- AD 1. Phalacrocorax [olivaceus]. This and auritus, two essentially allopatric species, comprise a superspecies (see van Tets, 1965). We feel that aristotelis (western Palearctic) is also a relative of these cormorants. Palmer (1962) has reviewed the races of auritus and olivaceus.
- AE 1. Anhinga [anhinga]. The members of this genus comprise a superspecies, although certain forms may be conspecific (Palmer, 1962; Vaurie, 1965a). In addition to anhinga the following species are included in the superspecies: rufa (largely Ethiopian), melanogaster (Southeast Asia) and novaehollandiae (Australian region).
- AF 1. Botaurus [stellatus]. B. lentiginosus is considered monotypic, following Palmer (1962). We tentatively list lentiginosus, stellatus, poeciloptilus (latter two Old World) and pinnatus (Middle and South America) as species comprising a superspecies, following Bock (1956). It re-

mains to be established whether stellatus and poeciloptilus are as closely related to lentiginosus as pinnatus appears to be. Possibly the Old World species form a species group with the New World forms, which would comprise a superspecies.

- AF 2. Ixobrychus [minutus]. Considerable variation occurs in I. exilis, with I. e. erythromelas (eastern South America) especially distinctive (Palmer, 1962; Norton, 1965). The closely related, geographical representatives exilis, sinensis (eastern Asia), and minutus (western Eurasia, Africa, Australia) are considered species comprising a superspecies (Bock, 1956).
- AF 3. Nycticorax [nycticorax]. We follow Bock (1956) in considering caledonicus (Australian region, southwest Pacific) as a species comprising a superspecies with N. nycticorax.
- AF 4. Nycticorax violaceus. We follow Bock (1956) in merging Nyctanassa (1887) in Nycticorax (1817). Relationships of this species are unclear, but it does not appear related to the South American Syrigma sibilatrix (Humphrey and Parkes, 1963; Short, 1969c; Bock, pers. comm., concurs). Wetmore (1946) described its variation.
- AF 5. Butorides [virescens]. The situation regarding contact between B. striatus (Old World, South America) and B. virescens in Panama is unclear but they seem to form a hybrid population (patens) (Eisenmann, pers. comm.) and could prove conspecific (Parkes, 1955). Pending studies to establish the nature of their contact we follow Bock (1956) and Wetmore (1965) in maintaining these species as components of a superspecies. Palmer (1962) discussed variation in virescens.
- AF 6. Bubulcus ibis. This recent entrant into the New World has reached the northeastern United States. Palmer (1962) discussed its variation. We consider the differences with Ardeola too great to justify congeneric status.
- AF 7. Egretta caerulea. The cogent arguments by Dickerman and Parkes (1968) for merger of various heron genera (including Florida, 1858) into Egretta (1817) seem reasonable, and follow from Bock (1956). We accept the merger.
- AF 8. Egretta rufescens. Dichromanassa (1878) is one of the genera merged into Egretta (see AF 7). This species is probably not as closely related to E. tricolor as Bock (1956) has indicated (Mayr, pers. obser.). Palmer (1962) discussed its variation.
- AF 9. Egretta tricolor. Variation in this species was considered by Palmer (1962).
- AF 10. Egretta [garzetta]. Leucophoyx (1894) is one of the genera merged in Egretta by Dickerman and Parkes (1968), and earlier by Bock (1956). E. thula, garzetta (Africa, Eurasia), and dimorpha (Madagascar) comprise a superspecies (Bock, 1956; see also Parkes, 1955). Palmer (1962) discussed variation in E. thula.

- AF 11. Egretta alba. Casmerodius (1842) is merged in Egretta (1817) by various authors (e.g., Bock, 1956; Vaurie, 1965a; Dickerman and Parkes, 1968). Although we also tentatively merge it in Egretta, further study is necessary to determine whether it is properly placed here or in Ardea as Meyerriecks (pers. comm.) believes; it may serve as a "bridge" connecting Egretta with Ardea.
- AF 12. Ardea [cinerea]. The gray or blue herons of this group occur throughout the world and it is somewhat a matter of convenience as to which should be considered full species comprising a superspecies, and which should be subspecies of a polytypic species A. cinerea. Mayr (1956) and Meyerriecks (1957, 1960) investigated the situation involving the Great White Heron ("occidentalis"). This forms an interesting case the Great White Heron is a peripheral Carribbean population in which the white morph, rare in mainland populations of Great Blue Herons, strongly predominates over the "normal" blue morph. The situation has been misinterpreted because the uncommon blue morphs of the Caribbean population were considered hybrids between a white and a blue "species." A. occidentalis clearly is conspecific with cinerea and interbreeds with A. c. wardi in southern Florida. We follow Parkes (1955) in treating herodias and cinerea (Old World) as conspecific. A. cocoi (South America) and A. melanocephala (Africa), and possibly A. pacifica (Australia), are component species of a superspecies with A. cinerea. Palmer (1962) discussed variation in A. cinerea.
- AG 1. Mycteria americana. This monotypic species has no very close relatives, but the generally accepted subfamilial status (Mycterinae) for Mycteria and Ibis is unwarranted because these "genera" are rather closely related to other storks (Kahl, pers. comm.).
- AH 1. Plegadis [falcinellus]. The essentially allopatric falcinellus and chihi are maintained as species, contra Palmer (1962), on the basis of sporadic, narrow overlap between them in Louisiana without interbreeding (Morony, MS.). The Andean ridgwayi is very closely related and possibly a member of the same superspecies. Variation in these ibises was discussed by Amadon and Woolfenden (1952) and by Palmer (1962).
- AH 2. Eudocimus albus. This monotypic ibis is essentially allopatric with very closely related E. ruber, but the two are apparently sympatric over a rather wide area in Colombia and Venezuela. We consider them as comprising a species group, although it is conceivable that this may represent a situation of color polymorphism. Eudocimus is doubtfully distinct from Plegadis.
- AH 3. Platalea ajaja. We do not consider this monotypic species sufficiently distinct to comprise a monotypic genus, particularly in view of the rather close relationship that obtains among Old World spoonbills. Hence, we merge Ajaia (1852) into Platalea (1758).
  - AI 1. Dendrocygna [bicolor]. Member of a superspecies with allo-

- patric, closely related arcuata of the eastern East Indies and Australian region (Delacour and Mayr, 1945). The superspecies is related to D. javanica (Johnsgard, 1965) which is sympatric with D. bicolor over a wide area of the Indian subcontinent. Delacour (1954) discussed variation in bicolor. The arrangement of the Anatidae herein follows Johnsgard (1965).
- AI 2. Dendrocygna autumnalis. Variation in this duck is discussed by Delacour (1954). It is apparently not very closely related to other whistling ducks (Johnsgard, 1965).
- AI 3. Cygnus cygnus. C. buccinator is considered conspecific with the Old World cygnus (Delacour and Mayr, 1945). It is related to C. columbianus (see AI 41). Delacour (1954) discussed its variation.
- AI 4. Cygnus columbianus. C. bewickii (Palearctic) and columbianus are considered conspecific, following Delacour and Mayr (1945); many authors consider them separate species. Variation of these forms was considered by Delacour (1954). This species is closely related to C. cygnus, forming with it a species group rather than a subgenus.
- AI 5. Anser fabalis. The three well-differentiated racial groups (brachyrhynchus, fabalis, and serrirostris groups) are characterized by Vaurie (1965a) and their variation discussed by Delacour (1954). (See AI 6.)
- AI 6. Anser albifrons. A variable species forming a species group with A. anser (Eurasia), A. fabalis, and A. erythropus (Eurasia) (Johnsgard, 1965). A. albifrons flavirostris is particularly well marked (for variation in this species see Delacour, 1954; Vaurie, 1965a).
- AI 7. Anser caerulescens. A. "hyperboreus" is regarded as a color morph of A. caerulescens (Delacour and Mayr, 1945; Cooke and Cooch, 1968). Variation in caerulescens was discussed by Delacour (1954) and by Vaurie (1965a).
- AI 8. Anser rossii. A diminutive goose which is closely related to A. caerulescens (Johnsgard, 1965). Polymorphism was discussed by Williamson (1957).
- AI 9. Anser canagicus. Following Delacour and Mayr (1945) Philacte (1870) is considered congeneric with Anser (1760).
- AI 10. Branta canadensis. Variation in this highly polytypic species was reviewed by Delacour (1954). The possibility exists that one of the well-differentiated forms such as hutchinsii may prove specifically distinct. B. c. hutchinsii and minima have not yet been shown to interbreed with adjacent (inland) and overlapping races. B. leucopsis appears to be closely related (Johnsgard, 1965).
  - AI 11. Branta leucopsis. Probably a close relative of B. canadensis.
- AI 12. Branta bernicla. We follow Delacour and Mayr (1945), Vaurie (1965a), and Johnsgard (1965) in considering well-differentiated nigricans conspecific with bernicla. There is only limited hybridization

between them (Manning, in Manning, Höhn and Macpherson, 1956), but interbreeding is probably limited only by factors cited by Vaurie (1965a). Variation in *bernicla* was discussed by Delacour (1954) and by Vaurie (1965a).

- AI 13. Aix sponsa. Closely related to Asian A. galericulata (Delacour and Mayr, 1945).
- AI 14. Anas [penelope]. Palearctic penelope and americana comprise a superspecies (Delacour and Mayr, 1945). With A. sibilatrix (South America) these form a fairly distinct group of ducks related to other species of Anas through A. strepera and A. falcata (Delacour, 1956; Johnsgard, 1965).
- AI 15. Anas strepera. There is a race, probably extinct, known from a few specimens from the Line Islands. The Gadwall is not closely related to other species of the genus although it may be nearest to A. falcata (Johnsgard, 1965).
- AI 16. Anas crecca. Palearctic crecca and carolinensis, often treated as species, are considered conspecific (Delacour and Mayr, 1945); they hybridize where they sporadically meet (Pribilof Islands; specimens in U. S. National Museum seen by Short). A. flavirostris of South America is particularly closely related to A. crecca (Johnsgard, 1965, considers them to comprise a superspecies), and African A. capensis and Asian A. formosa also appear closely related to crecca (Johnsgard, 1965).
- AI 17. Anas [platyrhynchos]. The mallards comprise an assemblage of closely related, largely allopatric forms which are difficult to treat some are well-marked subspecies (wyvilliana of Hawaii, laysanensis of Laysan Island, diazi, and fulvigula), one (rubripes) hybridizes extensively in a zone of overlap (Johnsgard, 1961b, 1967), and others (melleri of Madagascar, undulata of Africa, poecilorhyncha of southern and eastern Asia and the Australian region, and luzonica of the Philippines) apparently have diverged to the species level and are either wholly allopatric or overlap slightly (poecilorhyncha) with platyhrynchos with some hybridization. Our treatment essentially follows that of Delacour and Mayr (1945), Delacour (1956), and Johnsgard (1965). Delacour (1956) discussed variation in platyrhynchos.
- AI 18. Anas [acuta]. A. georgica of South America forms a superspecies with A. acuta (Delacour and Mayr, 1945). Its close relatives include A. bahamensis of the West Indies and South America and A. erythrorhyncha of Africa (Johnsgard, 1965). Delacour (1956) discussed variation in the races of acuta, which include the female-plumaged eatoni of Kerguelen Island and drygalskii of the Crozet Islands.
- AI 19. Anas discors. The Blue-winged Teal is monotypic (A. d. orphna is not sufficiently distinct to merit recognition) and related rather closely to A. querquedula (Palearctic) and A. cyanoptera (Delacour and Mayr, 1945; Johnsgard, 1965).

- AI 20. Anas cyanoptera. The Cinnamon Teal is rather closely related to A. querquedula and A. discors, and perhaps to the South American Shoveler (platalea). Delacour (1956) discussed its variation.
- AI 21. Anas clypeata. The shovelers comprise a species group, including clypeata, platalea (South America), smithi (Africa), and rhynchotis (Australasia). It is, however, equally possible that they are a polyphyletic group, large-billed birds having arisen repeatedly from blue-winged teal (Delacour and Mayr. 1945).
- AI 22. Aythya [ferina]. A. ferina of Eurasia and A. valisineria comprise a superspecies; Johnsgard (1965) noted their great similarity in behavior. Together with A. americana they comprise a species group (Delacour, 1959). A. valisineria represents a reinvasion of the New World by pochards, americana being an earlier derivative of this group.
- AI 23. Aythya americana. The Redhead and Common Pochard group (A. [ferina]) comprise a species group (Delacour and Mayr, 1945).
- AI 24. Aythya collaris. According to Johnsgard (1965) this species is related not to A. fuligula (Palearctic), but to the pochard group.
- AI 25. Aythya marila. Variation in the Greater Scaup was discussed by Delacour (1959). A. marila and A. affinis are very closely related, the former apparently representing a recent entrant into the Nearctic following the Wisconsin glaciation. We are not impressed by the great overlap of the two forms suggested by plotting their summer distributions; examination of the literature suggests that the significant contact and presumed overlap between them is mainly in the valleys of east-central Alaska (Gabrielson and Lincoln, 1959). Irving (1960) has provided meager data for their nesting sympatrically, and it is apparent from his discussion that from central Alaska to western Yukon there is a dramatic shift in occurrence and abundance from marila (west) to affinis (east). Throughout the breeding range of affinis outside of Alaska, marila appears to be an irregular or even rare breeding species. The two do not appear to interbreed, although it would be difficult to establish the identity of a hybrid; indeed many records of the occurrence of marila within the breeding range of affinis may represent misidentifications. We tentatively consider these as species forming a species group, but they may well comprise a superspecies (they could be designated an "emergent superspecies"). A. novae-seelandiae (New Zealand) and A. fuligula (Palearctic) are also very closely related to marila and affinis.
  - AI 26. Aythya affinis. (See AI 25.)
- AI 27. Somateria mollissima. Variation in the Common Eider was discussed by Delacour (1959); the Eurasian and North American group (mollissima group) of races is behaviorally (McKinney, 1961) and morphologically distinct from the Pacific (v-nigra) group. These forms do not quite meet in the central Canadian Arctic (Rand, 1948; Snyder, 1957). Their behavioral differences raise the question of possible repro-

ductive isolating mechanisms. S. mollissima is apparently most closely related to S. spectabilis (Johnsgard, 1965).

- AI 29. Somateria fischeri. This eider (Lampronetta) is merged in Somateria following Delacour and Mayr (1945).
- AI 30. Polysticta stelleri. This monotypic eider is somewhat different from the other eiders (Johnsgard, 1965).
- AI 31. Camptorhynchus labradorius. An extinct species which was probably a relative of eiders and scoters (Johnsgard, 1965; see also Humphrey and Butsch, 1958).
- AI 32. Histrionicus histrionicus. A monotypic species with no close relatives, but is probably related to the eiders (Johnsgard, 1965).
- AI 33. Clangula hyemalis. A species lacking close relatives (Johnsgard, 1965).
- AI 34. Melanitta nigra. This scoter is certainly congeneric with the other two species; its variation was discussed by Delacour (1959).
- AI 35. Melanitta perspicillata. Although probably closer to fusca than to nigra, the small size of the genus renders species groups unwarranted.
- AI 36. Melanitta fusca. Races of fusca are discussed by Delacour (1959) and by Vaurie (1965a). American deglandi is considered conspecific with fusca (Delacour and Mayr, 1945).
- AI 37. Bucephala albeola. Although somewhat distinct within the genus, the Bufflehead is not generically separable from the golden-eyes (Delacour and Mayr, 1945).
- AI 38-39. Bucephala islandica and B. clangula. The two golden-eyes are closely related and form a species group (Johnsgard, 1965). Delacour (1959) and Vaurie (1965a) discussed variation in clangula. The goldeneyes are closely related to Mergus cucullatus, as shown by Johnsgard (1961a) and demonstrated by the similarity of females of these species and by an adult male wild-taken hybrid of B. clangula × Mergus cucullatus in the U.S. National Museum (Short, pers. obser.; see Gray, 1958, for another such hybrid, and hybrids of M. albellus × B. clangula).
- AI 40. Mergus cucullatus. This merganser and its close relative M. albellus (Old World) connect the other mergansers with the golden-eyes (Bucephala; Johnsgard, 1961a; 1965, and see AI 38-39).
- AI 41. Mergus serrator. Races of the Red-breasted Merganser are weakly differentiated (see Delacour, 1959). (See AI 42.)
- AI 42. Mergus merganser. Forms a species group with M. serrator, M. squamatus (east Asia), and M. australis (Auckland Islands, extinct), according to Johnsgard (1965). Delacour (1959) discussed its variation.
- AI 43. Oxyura dominica. The monotypic Masked Duck now breeds regularly in southern Texas (Eisenmann, pers. comm). A tropical representative (Delacour, 1959) of the Ruddy Duck, it appears less specialized

than others of its genus (Johnsgard, 1965), and not especially closely related to any of the other stiff-tails.

- AI 44. Oxyura jamaicensis. Races of jamaicensis were discussed by Delacour (1959); the Andean ferruginea is very distinctive. A group of almost entirely allopatric, rufous-colored, blackish-headed stiff-tails occurs around the globe, including O. vittata (southern South America), O. maccoa (Africa), O. australis (Australian region), and O. leucocephala (Eurasia). These closely related forms (Johnsgard, 1965) conceivably could comprise a superspecies. However, the rather broad sympatry of vittata and O. j. ferruginea in southern South America suggests that the species are more distinct, and they are treated here as a species group.
- BA 1. Cathartes aura. Races of the Turkey Vulture were reviewed by Wetmore (1964). This species does not appear particularly closely related to any other species of Cathartes.
- BA 3. Vultur californianus. The California Condor seems related, albeit distantly, to the Andean Condor (V. gryphus). Fossil and extant species of this condor assemblage fall into three groups, presently considered genera (Vultur [1758], Gymnogyps [1842], and Pliogyps [1959]), but each of these appears to be comprised of but one species, or superspecies (see Fisher, 1944; Tordoff, 1959; Brodkorb, 1964). Allowing a reasonable degree of latitude in variation among congeneric species there seems to be no good reason why these condors should not be considered congeneric.
- BB 1. Elanus [caeruleus]. African and southern Asian caeruleus and notatus of Australia are closely related to leucurus (Vaurie, 1965a), and they are here regarded as comprising a superspecies. Parkes (1958) considered notatus and leucurus conspecific with caeruleus. Another species, E. scriptus, is similar to this group; it is sympatric with notatus in Australia. Friedmann (1950) considered variation in leucurus.
- BB 2. Elanoides forficatus. Races of this distinctive kite were discussed in Friedmann (1950) and characterized by Brown and Amadon (1968).
- BB 3. *Ictinia* [plumbea]. We consider plumbea (Neotropics) and the monotypic misisippiensis as geographically representative species comprising a superspecies. They may even prove conspecific, as suggested by Sutton (1944).
- BB 4. Rostrhamus sociabilis. Races of the Snail Kite were discussed in Friedmann (1950) and characterized in Brown and Amadon (1968). Rostrhamus (Helicolestes) hamatus of northern South America is a relative (Amadon, 1964).
- BB 5. Accipiter [gentilis]. The related, allopatric goshawks A. mèlanoleucus (Africa), A. meyerianus (Southwest Pacific), and probably A. henstii of Madagascar comprise a superspecies with A. gentilis (Voous, 1960; Amadon, 1964). Variation in gentilis is treated in Friedmann

- (1950) and in Vaurie (1965a). Among recent authors Todd (1963) considered the New World forms (atricapillus) specifically distinct from gentilis.
- BB 6. Accipiter [nisus]. Variation in this species is covered in Friedmann (1950) and in Storer (1952). We follow Storer, and Brown and Amadon (1968) in considering the well-marked erythrocnemius (southern South America), ventralis (northern South America), and chionogaster (Central America) conspecific with striatus. The Eurasian A. nisus and A. striatus comprise a superspecies with A. rufiventris (Africa) and A. madagascariensis (Madagascar), and possibly others, as suggested by Stresemann (1924; see also Friedmann, 1950).
- BB 7. Accipiter [bicolor]. The allospecies bicolor (Neotropics), cooperii, and gundlachi (Cuba) comprise a superspecies (Amadon, 1964). Relationships of this superspecies are perhaps with the nisus group but they remain to be fully elucidated.
- BB 8. Buteo nitidus. This hawk and B. magnirostris (Middle, South America) are isolated among the buteos (Amadon, 1965; Brown and Amadon, 1968). The Gray Hawk may be related within the genus to the lineatus group (Johnson and Peeters, 1963). B. nitidus and B. magnirostris possibly comprise a species group, but nitidus may be more distinct, possibly connecting Buteo with other genera (Amadon, 1965). Races of nitidus were discussed in Friedmann (1950) and characterized in Brown and Amadon (1968). The arrangement of the genus Buteo herein follows that of Amadon (1965).
- BB 9. Buteo lineatus. Racial variation in this buteo was covered in Friedmann (1950) and in Brown and Amadon (1968). B. lineatus and B. ridgwayi (Hispaniola), and possibly B. leucorrhous (South America), form a species group perhaps related to B. magnirostris (Brown and Amadon, 1968). Bond (1957) considered ridgwayi nearer to magnirostris than to lineatus.
- BB 10. Buteo platypterus. Relationships of the Broad-wing are uncertain, but it may be related to the *lineatus* group (Johnson and Peeters, 1963; Amadon, 1965). Its variation was discussed by Friedmann (1950).
- BB 11. Buteo brachyurus. We tentatively follow Amadon (1964) in considering the Andean albigula conspecific with brachyurus. Lehmann and Haffer (1960) reported them occurring sympatrically, but they appear to be altitudinally separated (Amadon, pers. comm.).
- BB 12. Buteo swainsoni. This monotypic hawk appears related to B. [albicaudatus] (Amadon, 1965).
- BB 13. Buteo [albicaudatus]. The hawks Buteo albicaudatus, polyosoma, poecilochrous, and galapagoensis are closely related (Vaurie, 1962; Brown and Amadon, 1968), and comprise a superspecies probably related to B. swainsoni (Amadon, 1965). Friedmann (1950) discussed variation in B. albicaudatus.

- BB 15. Buteo [buteo]. The red-tailed "buzzards" comprise a cosmopolitan group of allopatric, closely related species including B. jamaicensis, B. buteo (Eurasia), B. ventralis (southern South America), B. oreophilus (Africa), and B. brachypterus (Madagascar). These are believed to comprise a superspecies (Amadon, 1964; Vaurie, 1965a). Of these, buteo and ventralis have been considered conspecific with jamaicensis and this may prove to be correct. We follow various authors (most recently Brown and Amadon, 1968) in merging the western, melanic harlani as a race of jamaicensis, although its status remains to be elucidated fully. The considerable variation in jamaicensis was discussed by Taverner (1936), Friedmann (1950) and was summarized recently by Brown and Amadon (1968). The closest relative(s) of this superspecies is not readily apparent, but perhaps may be rufinus or regalis.
- BB 16. Buteo lagopus. Cade (1955) and Vaurie (1961c) described the variation in this buteo. Its relationships are unclear.
- BB 17. Buteo regalis. This monotypic species is usually placed beside B. lagopus, but it does not appear closely related to that species. Rather, it may be related to the buteo group through Mediterranean-Asian B. rufinus (Voous, 1960), or to east Asian hemilasius (fide Amadon).
- BB 18. Parabuteo unicinctus. Variation in this distinctive buteo was treated by Friedmann (1950).
- BB 19. Buteogallus [aequinoctialis]. We follow Amadon (in Brown and Amadon, 1968) in considering the controversial subtilis (southern Middle America, South America) a subspecies of B. anthracinus and the latter as comprising a superspecies with the coastal South American aequinoctialis. Monroe (1968) argued that subtilis is specifically distinct, and if it proves to be so, it will constitute another element of this superspecies. There appears to be slight sympatry between anthracinus and aequinoctialis between the mouth of the Orinoco River and Guyana (Meyer de Schauensee, 1966). Brown and Amadon (1968) discussed variation in anthracinus.
- BB 20. Aquila chrysaetos. Variation in the Golden Eagle has been reviewed by Friedmann (1950), Vaurie (1965a), and summarized by Brown and Amadon (1968). Its relationships remain to be established, but audax of Australia may be its closest relative and conceivably could even comprise a superspecies with chrysaetos. A. verreauxi (Africa) may also be closely related to chrysaetos (Amadon, pers. comm.).
- BB 21. Haliaetus [albicilla]. Among the white-tailed sea eagles, leucocephalus and albicilla are closely related, possibly even conspecific (Voous, 1960). They are treated here as components of a superspecies. Variation in leucocephalus was discussed by Friedmann (1950). Relationships of this superspecies with other sea eagles is uncertain.
- BB 22. Circus [cyaneus]. We follow Amadon (1961) in considering cinereus (South America) specifically distinct from cyaneus, although

they may prove conspecific. They are here treated as comprising a superspecies. Variation in *cyaneus* was considered by Friedmann (1950) and by Brown and Amadon (1968). The New World *hudsonius* and Old World *cyaneus* groups are sometimes considered specifically distinct. Relationships among the harriers are not sufficiently clear to establish a species group.

- BC 1. Pandion haliaetus. Variation in the Osprey was treated by Friedmann (1950) and summarized by Brown and Amadon (1968).
- BD 1. Polyborus plancus. We follow Brown and Amadon's (1968) merger of plancus and cheriway, which seem to intergrade (Amadon, 1964). Brown and Amadon further remarked (p. 736): "Now that P. cheriway is regarded as a race of P. plancus it would be no great extension to include lutosus also." The latter, an extinct form from Guadalupe Island, is often considered a separate species, but we include it here with plancus. Polyborus is used as the generic name (Amadon, 1954); since the genus now becomes monotypic, the very closely related (Brown and Amadon, 1968) genus Phalcobaenus probably could be merged into Polyborus.
- BD 2. Falco [rusticolus]. F. rusticolus and the Asian F. altaicus tentatively are considered to comprise a superspecies. Dementiev (1947) considered them very closely related but not conspecific. However, Amadon (pers. comm.) considers altaicus closer to F. cherrug. The gyrfalcon group includes F. mexicanus, F. biarmicus (Africa, Mediterranean), F. jugger (India), and F. cherrug (eastern Europe to Central Asia), following Brown and Amadon (1968). Variation in F. rusticolus is slight; Vaurie (1961b) considered the species monotypic.
- BD 3. Falco mexicanus. The Prairie Falcon is strikingly like F. jugger of the Indian subcontinent (Meinertzhagen, 1954); F. biarmicus is also very similar (Vaurie, 1961b). These species are part of the rusticolus group (see BD 2) and probably owe their similarities to parallel evolution after independent origin from a rusticolus-like ancestor, rather than to direct relationship.
- BD 4. Falco [peregrinus]. The peregrines comprise a cosmopolitan group of falcons, including rare and little known kreyenborgi (southern South America), fasciinucha (Africa), and Neotropical deiroleucus, as well as peregrinus (Brown and Amadon, 1968). We consider these as representing a superspecies related to the gyrfalcons. It is possible that one or more of these (especially kreyenborgi) may prove conspecific with peregrinus. On the other hand, further study of fasciinucha may prove it to overlap widely with peregrinus, and thus necessitate its exclusion. The well-differentiated pelegrinoides (Canary Islands, northwestern Africa, and Turkestan) is considered by some authors (Dementiev and Iljitschev, 1961; Vaurie, 1961a) to be a separate species, and if so it would constitute part of this superspecies. Races of peregrinus were discussed by

Vaurie (1961a) and White (1968), and were summarized by Brown and Amadon (1968).

- BD 5. Falco femoralis. Variation in this falcon was treated by Friedmann (1950) and summarized by Brown and Amadon (1968). The relationship of femoralis with other hobbies remains to be established.
- BD 6. Falco columbarius. Races of columbarius vary greatly in color but the variation mainly involves intensity of melanin pigments. Friedmann (1950), Vaurie (1961b), and Brown and Amadon (1968) reviewed this variation. The affinities of this falcon possibly may lie with chicquera of India and Africa, but the two taxa are not closely related (Brown and Amadon, 1968).
- BD 7. Falco [tinnunculus]. F. sparverius is the New World representative of the tinnunculus group (Voous, 1960), here considered to comprise a superspecies. Following Brown and Amadon (1968) we include within this superspecies Eurasian tinnunculus, East Indian moluccensis, Australian cenchroides, newtoni of Madagascar, punctatus of Mauritius, araea of the Seychelle Islands, and sparverius. The closely related kestrels rupicoloides (Africa), Mediterranean and central Asian naumanni, and West African alopex comprise a species group with F. [tinnunculus]. The subspecies sparveroides of Cuba and caribaearum of the southern West Indies are well differentiated. Races of sparverius were discussed in Bond (1943), Moore and Bond (1946), and Friedmann (1950); Vaurie (1965a) covered variation in tinnunculus and Brown and Amadon (1968) characterized all species and races cited here.
- BE 1. Ortalis [vetula]. There is considerable diversity in the treatment of the species of Ortalis, stemming largely from their essentially allopatric distribution. O. poliocephala (southwestern Mexico) was treated by Friedmann, et al. (1950), as a race of O. vetula, but Moore and Medina (1957), merging O. "wagleri" (Mexico) in poliocephala, convincingly argued that the latter is not conspecific with vetula. L. I. Davis (1965) concurred with the findings of Moore and Medina, and considered poliocephala, vetula, and leucogastra (southern Mexico to Nicaragua) as separate species. Vuilleumier (1965) treated O. poliocephala, O. vetula, O. ruficrissa (northern South America), and O. ruficauda (northern South America) as comprising a superspecies; Vaurie (1965b, 1968), however, considered O. vetula, O. garrula (Caribbean coast from Honduras to Colombia), and O. ruficauda as comprising a superspecies. Short (pers. obser.) is inclined to feel that poliocephala and vetula are closely related. The significant point is that their relationships are not clear; it is possible, as suggested by Amadon (pers. comm.), that Ortalis might even comprise but a single superspecies. Our tentative arrangement follows that of Vuilleumier, with garrula excluded because of its apparent lack of the typical "chachalaca" vocalization otherwise found throughout the group (Amadon, pers. comm.).

- BF 1. Dendragapus obscurus. The obscurus and fuliginosus groups differ in many respects (Hoffmann, 1956; Short, 1967b), and they were long maintained as separate species before Peters (1934) merged them. This merger was followed by the A.O.U. Check-list Committee (1944). Contacts between the two groups are limited by topography and habitat to a narrow area in Washington and British Columbia where some interbreeding occurs (Munro and Cowan, 1947; Jewett, et al., 1953).
- BF 2. Dendragapus canadensis. Canachites Stejneger, 1885, and Falcipennis Elliott, 1864, are considered synonyms of Dendragapus Elliot, 1864 (Short, 1967b). The distinctive canadensis and franklinii groups of D. canadensis were considered separate species for many years (see, e.g., A.O.U. Check-lists through the fourth edition, and Peters, 1934). They were merged by the A.O.U. Check-list Committee (1955) following the suggestion by Aldrich in Jewett, et al. (1953). Hybridization occurs on a large scale in southwestern Alberta and north-central British Columbia, as noted by Aldrich (specimens in U. S. National Museum).
- BF 3. Bonasa umbellus. This clinally variable and polymorphic species was the subject of a taxonomic review by Aldrich and Friedmann (1943). The Ruffed Grouse is related to Palearctic Bonasa bonasia and B. sewerzowi (Short, 1967b), and forms a species group with them.
- BF 4. Lagopus lagopus. Included as conspecific is the Red Grouse (L. "scoticus") of the British Isles (Short, 1967b).
- BF 5. Lagopus mutus. A highly polytypic species which includes various distinctive and non-clinal races (e.g., evermanni and rupestris in North America) that conceivably could represent semispecies. Racial characters are contained in Ridgway and Friedmann (1946).
- BF 6. Lagopus leucurus. This distinct species was characterized racially by Ridgway and Friedmann (1946).
- BF 7. Tympanuchus cupido. Tympanuchus "pallidicinctus" is considered conspecific with cupido (Short, 1967b) because of: (1) their great similarity contrasted with the much greater differences between T. cupido and T. phasianellus, which hybridize with some frequency (Johnsgard and Wood, 1968); (2) their allopatry and the occurrence of pallidicinctus in a region (high southern plains) where slight differentiation and almost no endemism characterize the fauna; and (3) the variation within and among T. c. cupido, T. c. pinnatus and T. c. attwateri (see Ridgway and Friedmann, 1946; Short, 1967b) is barely extended by inclusion of pallidicinctus within T. cupido (See BF 8.)
- BF 8. Tympanuchus phasianellus. "Generic" characters separating Tympanuchus (1842) and "Pedioecetes" (1858) are but those one would expect to mark sympatric, interacting, congeneric species. Hybridization between cupido and phasianellus is relatively frequent (Mayr, 1963; Gray, 1958, lists hybrids between T. cupido and three different races of T.

- phasianellus; see Johnsgard and Wood, 1968). Racial characteristics are given by Ridgway and Friedmann (1946).
- BF 9. Centrocercus urophasianus. Races of this peculiar species, which has no close relatives, were discussed by Ridgway and Friedmann (1946).
- BG 1. Colinus virginianus. There are many races, some well differentiated, of this species (Ridgway and Friedmann, 1946). The "genus" Colinus is probably only a superspecies, but studies are needed to establish this. All forms of Colinus are allopatric. At present four species are recognized, but nigrogularis (Yucatán to Honduras) is probably conspecific with virginianus, and leucopogon (western Central America) has been merged with cristatus (South America north to western Panama) by Hellmayr and Conover (1942), as well as by Monroe (1968).
- BG 2. Callipepla squamata. The races of this species were characterized by Ridgway and Friedmann (1946). This quail apparently hybridizes occasionally with sympatric C. gambelii, and backcrossing may occur (Hubbard, 1966).
- BG 3. Callipepla [californica]. The species californica and gambelii, possibly conspecific, comprise a superspecies. They are allopatric, meeting very narrowly and hybridizing occasionally (Henshaw, 1885) in southern California. Lophortyx (1838) was merged in Callipepla (1832) by Phillips, et al. (1964). Gray (1958) listed wild-taken hybrids of Callipepla × Lophortyx (as well as of Oreortyx × Lophortyx, Colinus × Callipepla and Colinus × Lophortyx). It may be that recognition of Colinus as a superspecies (see BG 1) will be a prelude to merger of all of these "genera" into Colinus (1820), which would then contain about seven species (see also Johnsgard, 1970). Racial variation in californica and gambelii was discussed by Ridgway and Friedmann (1946; see also Short and Crossin, 1967).
- BG 4. Callipepla picta. Characters of the races are contained in Ridgway and Friedmann (1946). Phillips, et al. (1964: 29) suggested that "probably the genera Callipepla and Oreortyx (1858) should be united." This species forms a species group with Callipepla [californica] and C. douglasii.
- BG 5. Cyrtonyx [montezumae]. This superpsecies is comprised of C. montezumae, C. sallei (western Mexico), and C. ocellatus (southern Mexico to Nicaragua). All are allopatric and Peters (1934:57) stated that "sallei and ocellatus are both representative forms of montezumae and should perhaps be regarded as subspecies of the latter." Ridgway and Friedmann (1946) merged sallei into montezumae, but left ocellatus as a species. The latter authors characterized the races of these species (see also Phillips, 1966).
- BH 1. Meleagris gallopavo. Racial characters were presented by Ridgway and Friedmann (1946). Only one extant species. (Agriocharis is possibly congeneric, but not very closely related to M. gallopavo.)

- CA 1. Grus americana. Relationships among species of Grus are poorly understood. G. americana may be closely related to G. japonensis, and is probably somewhat closer to G. grus (Palearctic) than is G. canadensis.
- CA 2. Grus canadensis. This species appears not to be closely related to others of its genus. Racial variation has been discussed by Walkinshaw (1949, 1965).
- CC 1. Rallus [longirostris]. Rallus longirostris and R. elegans are respectively saltwater and freshwater forms that replace each other ecologically in eastern North America. They interbreed at least occasionally where they meet (Meanley and Wetherbee, 1962). Freshwater Mexican and western North American coastal forms have been considered recently both as R. elegans (Hellmayr and Conover, 1942) and as R. longirostris (Friedmann, et al., 1950). Warner and Dickerman (1959) followed Hellmayr and Conover, but question the status of these supposed "species." The West Coast races (obsoletus group), which have in the past occasionally been considered specifically distinct, are included here within longirostris, but their relationship with freshwater and saltwater forms elsewhere remains uncertain.
- CC 2. Rallus [aquaticus]. Rallus aquaticus (Palearctic) and R. limicola are closely similar (Voous, 1960) and are best regarded as comprising a superspecies. Recordings of their vocalizations indicate points of similarity (certain calls, such as the long, repeated, metallic "peek" series) by which both differ from the longirostris group and other genera here considered.
- CC 3. Porzana carolina. Voous (1960) has noted the similarity of P. carolina and P. porzana. Short feels that Australian fluminea may be related closely to both carolina and porzana.
- CC 4. Coturnicops noveboracensis. C. n. goldmani is a moderately well defined race known only from the Lerma Valley marshes of central Mexico. We are uncertain whether "Coturnicops" is related to Porzana or to Laterallus (e.g., through L. spiloptera), but in any event Coturnicops (Porzana) exquisita of eastern Asia is closely related to noveboracensis, as noted by Vaurie (1965a and pers. comm.). Indeed, these may comprise a superspecies. C. notata of South America is not as closely related to noveboracensis as is the latter to exquisita.
- CC 5. Laterallus jamaicensis. L. "spilonotus" (Galapagos Islands) appears to be a melanic form of L. jamaicensis (Short, pers. obser.), probably conspecific with, but possibly specifically distinct from the latter.
- CC 7. Gallinula chloropus. This species appears related most closely to G. tenebrosa (Australia) and G. angulata (Africa); the latter was considered a sibling species of chloropus by Voous (1960). The South American races garmani and galeata, and brachyptera of Africa appear quite distinct morphologically.

- CC 8. Fulica [atra]. F. atra (Palearctic) and F. americana are closely related and possibly conspecific. Bond (1945, 1950) reported interbreeding of F. americana and the West Indian F. caribaea, with which it narrowly overlaps, and which also appears to be a representative form of this superspecies. Gill (1964) has shown that F. "ardesiaca" (Andes Mountains) is a morph of F. americana. Gill (in litt.) agrees that atra is very closely related to americana, especially considering the americanacaribaea relationship, and that F. leucoptera (southern South America) is apt to be the representative of the atra superspecies among the three species found in its region. Thus, these four species appear to comprise a superspecies.
- CD 1. Charadrius [hiaticula]. We tentatively maintain hiaticula and semipalmata as comprising a superspecies pending further study of their interbreeding (Smith, 1969; see also Vaurie, 1965a) on Baffin Island. Smith's evidence suggests that they are not interbreeding freely, but are conspecific morphs. Interbreeding may also occur on the Chukotski Peninsula of Siberia (Bock, 1959), but the situation there is unclear. C. placidus seems to be a close relative of this superspecies as Bock (1959) has suggested.
- CD 3. Charadrius [alexandrinus]. The forms C. marginatus (Ethiopia), C. occidentalis (South America), and C. ruficapillus (Australia) were merged into C. alexandrinus by Peters (1934), followed by Bock (1958). Vaurie (1964, 1965a) regarded occidentalis as a race of C. alexandrinus, and marginatus as a close relative of the latter. We recognize these forms tentatively as species within the superspecies C. alexandrinus, although one or more of the forms may prove to be only subspecifically distinct. This superspecies appears to be closely related to C. collaris and possibly to C. melodus.
- CD 6. Charadrius montanus. The relationships of this complex, including C. veredus (eastern Asia) and C. asiaticus (central Palearctic region) were discussed by Bock (1958) and by Vaurie (1964, 1965a). Certainly all are closely related, and they perhaps comprise a superspecies. The complex appears related to C. mongolus (Palearctic) on the one hand and to the dotterels (Eudromias morinellus of the Palearctic and E. modestus of South America) on the other hand.
- CD 8. *Pluvialis dominica*. The relationships of the golden plovers are unclear. *P. dominica* and *P. apricaria* (western Palearctic) prefer different habitats, but they are largely allopatric and have hybridized at least once (Vaurie, 1964). They may comprise a superspecies, but are here considered as comprising a species group.
- CE 1. Arenaria [interpres]. The two species of Arenaria appear to comprise a superspecies. They are narrowly sympatric in western Alaska (Gabrielson and Lincoln, 1959), and breeding birds of both species have been collected from certain areas with no indication of hybridization (specimens in U. S. National Museum, Short, pers. obser.). Their downy

- young are fairly distinctive and easily distinguishable. Their relationships within the sandpipers are uncertain (perhaps tringine according to Jehl, 1968b), but they appear to belong within this group. Kozlova (1962) discussed some relationships within this family.
- CE 2. Scolopax minor. The American Woodcock does not appear generically (Philohela, 1841) separable from Scolopax (1758). Although biologically "good" species, S. minor and S. rusticola (Palearctic) are obviously closely related, geographical representatives. S. mira of the Ryukyu Islands (Amami-Oshima), which may be specifically distinct from rusticola, is also included in this group.
- CE 3. Gallinago gallinago. Relationships among snipe are very uncertain and further studies are needed to determine whether South American paraguaiae and African nigripennis are members of the same polytypic species (gallinago) as indicated here and suggested by Vaurie (1965a), or comprise a superspecies. North American G. gallinago delicata differs from Old World forms of G. gallinago in characteristics cited by Todd (1963).
- CE 4. Numenius [arquata]. This superspecies includes the very similar (Voous, 1960) N. americanus and Palearctic N. arquata, which we consider closely related. N. madagascariensis appears related to this superspecies, but how closely related we are not certain. Oberholser (1918c) discussed the races of americanus.
- CE 5. Numenius phaeopus. N. phaeopus appears closely related to N. tahitiensis, and possibly also to tenuirostris (central Palearctic). There may be no sympatry between phaeopus and tahitiensis (Gabrielson and Lincoln, 1959), but this does not necessarily indicate that these species comprise a superspecies. We maintain the three species as a species group within Numenius.
  - CE 6. Numenius tahitiensis. (See CE 5.)
- CE 7. Numenius [borealis]. As Vaurie (1965a) and others have noted, borealis is closely related to Palearctic N. minutus. Their relationship may not be so close as to warrant considering them conspecific, as did Vaurie. We prefer to retain them as species comprising a superspecies.
- CE 10. Tringa [incana]. T. incana and T. brevipes (Siberia) appear to comprise a superspecies. Vaurie (1965a) discussed their characters and he considered them separate species on the basis of their reported sympatry in Siberia. We agree with Vaurie's merger of Heteroscelus (1858) into Tringa (1758).
- CE 11. Tringa hypoleucos. We follow Voous (1960), Vaurie (1965a), and other authors in merging Actitis (1811) into Tringa (1758). North American macularia and Palearctic hypoleucos are considered conspecific for reasons presented by Voous (1960). These allopatric forms are certainly closely related, at least comprising a superspecies, but they are more than likely conspecific.

- CE 12. Tringa [ochropus]. T. solitaria is tentatively considered a geographic representative of T. ochropus following various authors. T. glareola appears to be related to this superspecies. Races of solitaria were discussed by Conover (1944b) and by Todd (1963). L. Oring (pers. comm.) considers solitaria nearer to glareola than to ochropus.
- CE 13. Tringa [nebularia]. T. melanoleuca appears to be the closely related geographical replacement of T. nebularia (Palearctic) in North America (Voous, 1960). We agree with many authors in merging Totanus (1803) in Tringa (1758).
- CE 14. Tringa flavipes. The relationships of this yellowlegs are unclear, but T. erythropus and T. totanus may be related to it.
  - CE 15. Limosa fedoa. The relationships of this species are not clear.
- CE 16. Limosa lapponica. The relationships of this species are unclear.
- CE 17. Limosa [limosa]. Limosa haemastica appears closely related to Palearctic L. limosa, and the two are geographical representatives. We agree with Voous (1960) that they are not conspecific, however.
- CE 18. Limnodromus [griseus]. The arguments of Pitelka (1950) for separate species status of L. griseus and L. scolopaceus are not fully convincing, but we retain them as species within a superspecies for the time being. Rand (1950; see also Vaurie, 1965a) demonstrated that Pitelka (1948) was incorrect in generically separating L. semipalmatus of Siberia from the other two dowitchers; Rand (1950) believed that these three forms are geographical representatives. We feel that semipalmatus is not as closely related to griseus and scolopaceus as the latter are to one another. Pitelka (1950) reviewed the races of griseus and characterized L. griseus and L. scolopaceus.
- CE 19. Calidris canutus. The taxonomy of this species was discussed by Conover (1943) and by Todd (1963). The genus Calidris (1804) presented here is that of Voous (1960) and of Kozlova (1962). It is nearly that of the British Ornithologists' Union Check-list (1952), and includes the genera Erolia (1816), Ereunetes (1811), and Crocethia (1828) of the A.O.U. Check-list (1957). Certain groupings reflect the work of Pitelka and his students. Even Micropalama and possibly Tryngites may ultimately be included in Calidris.
- CE 20. Calidris [maritima]. We feel that the differences between maritima and ptilocnemis are sufficiently great to warrant specific status for each (see Vaurie, 1965a), although we recognize their close relationship and the fact that they are geographical representatives by their treatment as a superspecies. Conover (1944a) discussed races of ptilocnemis, and considered the latter as a separate species.
- CE 21. Calidris alpina. See Todd (1953) for a discussion of the races of this species.
  - CE 25. Calidris melanotos. This species may comprise a species

- group with C. ferruginea (Siberia), perhaps C. acuminata (Palearctic), and possibly C. fuscicollis (Holmes and Pitelka, 1964).
- CE 27-28. Calidris pusilla and C. mauri. The former genus Ereunetes comprises a species group.
  - CE 29. Calidris alba. (See CE 19.)
  - CE 30. Micropalama himantopus. (See CE 19.)
  - CE 31. Tryngites subruficollis. (See CE 19.)
- CE 32. Aphriza virgata. This peculiar species seems definitely a scolopacid, probably related to the calidrine sandpipers (Jehl, 1968b), and not related closely to Arenaria, with which it is usually allied. Hence, we have removed it from the vicinity of Arenaria, placing it near the calidrine sandpipers.
- CF 1. Recurvirostra [avosetta]. The avocets appear to comprise a superspecies. One or more forms may prove to be conspecific with another, but pending further study all are treated as species. These are R. avosetta (Palearctic), R. americana, R. andina (South America), and R. novaehollandiae (Australia).
- CF 2. Himantopus [himantopus]. We tentatively consider eight species as comprising a superspecies, believing that this is a better course than partial, dubious lumping with insufficient knowledge. The species are H. himantopus (Palearctic, Africa, and continental Asia), H. melanurus (South America), H. mexicanus, H. ceylonensis (Ceylon), H. leucocephalus (East Indies to New Zealand), H. knudseni (Hawaiian Islands), H. novaezelandiae (New Zealand), and H. meridionalis (South Africa). Some of these will undoubtedly prove conspecific.
- CG 1-3. Phalaropus fulicarius, P. lobatus, and P. tricolor. There appear to be no trenchant characters warranting retention of monotypic genera for the three phalaropes. We follow the British Ornithologists' Union Check-List (1952), Voous (1960), Vaurie (1965a), and others in considering them congeneric. Their interrelationships are unclear, but lobatus and fulicarius are probably related to each other more closely than either is to tricolor (see Bull, 1964).
- CI 1. Larus atricilla. The species is largely coastal but breeds occasionally around Salton Sea (Grinnell and Miller, 1944). Variation in the Laughing Gull is slight and we follow the A.O.U. Check-list (1957) in not recognizing subspecies of it (see Parkes, 1952a). Treatment of gulls and terns largely follows that of Moynihan (1959).
- CI 3. Larus philadelphia. It is unclear whether the relatives of philadelphia (Palearctic ridibundus, brunneicephalus of Siberia, serranus of South America, maculipennis of southern South America, and possibly others like genei of the Mediterranean region) comprise with it a superspecies (possibly some are even conspecific) or merely a species group as we tentatively treat them. These hooded gulls are allopatric and closely

related (Moynihan, 1959). Stegmann (1935) has indicated that brunneicephalus and ridibundus interbreed.

CI 4. Larus sabini. This species (genus Xema, 1819), was merged into Larus (1758) by Moynihan (1959), Vaurie (1965a), and others. Its races are very poorly defined (Salomonsen, 1951; Todd, 1963). L. furcatus (Neotropics) possibly is closely related (Moynihan, 1959). Although largely coastal, the species does breed inland (Snyder, 1957; Gabrielson and Lincoln, 1959).

CI 5-6. Larus delawarensis and L. canus. These species appear closely related and are treated as comprising a species group. Johansen (1961) considered them as a superspecies, including the Siberian L. kamtschatschensis.

CI 7-12. Larus hyperboreus, L. californicus, L. glaucescens, L. argentatus, L. thayeri, and L. glaucoides. These large gulls provide one of the most complicated situations in avian taxonomy at the species level. Despite recent, effective studies by Kist (1961), Macpherson (1961), and N. G. Smith (1966), the gaps in our knowledge still render their relationships difficult to interpret (Short, 1969a). Even in the limited regions where studies have been conducted problems remain, as, for example, the explanation for the excessive variation in "Kumlien's" Gull (N. G. Smith, 1966; Sutton, 1968). There is no question of the very close relationship of L. thayeri, L. argentatus, and L. glaucoides which exist in at least limited sympatry—yet what about schistisagus (east Siberia) and glaucescens, both of which hybridize with some frequency with argentatus? Portenko (1963; see also Vaurie, 1965a) considered schistisagus and argentatus conspecific on the basis of their interbreeding in southern Koryakland (Siberia). Williamson and Peyton (1963; Williamson, unpublished) discussed the interbreeding of glaucescens with argentatus in Alaska, and the relations of these forms with schistisagus. Barth (1968) has recently suggested the merger of all of these forms into L. argentatus. In Europe both L. fuscus and L. "cachinnans" interbreed with forms of argentatus (Voous, 1960; Barth, 1968). Some of these hybridizing forms are morphologically as different from each other in their characters as those forms occurring sympatrically with little or no interbreeding in the Baffin Island region. L. occidentalis is also involved in this complex, as is hyperboreus (which interbreeds with argentatus in Iceland). It would be premature to attempt definition of a superspecies at the present time. We consider these species as comprising a species group, recognizing that some elements are apt to prove more closely related than are others. Moynihan (1959) noted the similarities of this species group with L. delawarensis through L. californicus, and L. marinus is not very far from them. Various races of hyperboreus, glaucoides, and argentatus were discussed by Oberholser (1918f), Rand (1943), Vaurie (1965a), N. Smith (1966), and Barth (1968).

CI 13. Larus [marinus]. L. marinus and L. dominicanus have been

- considered conspecific by Hellmayr and Conover (1948). They were viewed as closely related geographical representatives by Wetmore (1926) and by Stegmann (1934). We tentatively consider them to form a superspecies, pending study of their relationships.
- CI 14. Rynchops nigra. It is unclear whether R. flavirostris of Africa and R. albicollis of southern Asia comprise with nigra a species group or a superspecies.
- CI 15. Sterna nilotica. Gelochelidon (1830) is merged in Sterna (1758) following Moynihan (1959).
- CI 16. Sterna caspia. Hydroprogne (1829) is merged in Sterna following Moynihan (1959) and Voous (1960).
- CI 17. Sterna hirundo. Sterna hirundo is very similar to S. paradisaea, and these species occupy adjacent, virtually allopatric ranges (see Todd, 1963). Nonetheless, they probably are not very closely related, but are rather indirectly related through Southern Hemisphere terns (S. vittata, S. virgata, and S. hirundinacea) of this group (Murphy, 1938). Asiatic S. h. longipennis is well differentiated and was excluded from hirundo by early authors.
- CI 18. Sterna paradisaea. Relationships of this tern within the hirundo group are unclear (see CI 17), but S. vittata of the Southern Hemisphere may be its nearest relative (Murphy, 1936, 1938).
- CI 20. Sterna [albifrons]. The relationships of S. superciliaris (eastern South America), S. lorata (western South America), and S. nereis (Australian region) with albifrons are unclear. Moynihan (1959) considered that these comprise a superspecies. Races of albifrons were discussed by Burleigh and Lowery (1942a), and by Friedmann, et al. (1950).
- CI 21. Chlidonias niger. The marsh terns C. niger, C. leucopterus (southern Europe to eastern Asia), and C. hybrida (southern Europe to eastern Asia) constitute a group of closely related species perhaps not separable generically from Sterna (Moynihan, 1959). Moynihan considered hybrida intermediate between niger and leucopterus and the black-capped terns (Sterna).
- DA 1. Columba leucocephala. The genus has been reviewed by Goodwin (1959) and by Johnston (1962). Both authors considered speciosa (Mexico to South America) as closely related to this species, although Goodwin more recently (1967) regarded West Indian C. squamosa as more closely related to leucocephala than is speciosa. C. squamosa and C. leucocephala are partly sympatric.
- DA 2. Columba [fasciata]. We follow Goodwin (1959) and Johnston (1962) in considering fasciata, araucana (southern South America), and caribaea (West Indies) as comprising a superspecies. Following Johnston, albilinea is merged in fasciata. Brodkorb (1943) discussed variation in C. fasciata.
  - DA 3. Columba [inornata]. We follow the suggestion of Goodwin

- (1959) and of Johnston (1962) that C. flavirostris, C. inornata (West Indies), and C. oenops (Peru) comprise a superspecies.
- DA 4. Zenaida asiatica. This species, quite closely related to the macroura group, is the subject of a recent revision by Saunders (1968).
- DA 5. Zenaida [macroura]. The former genus Zenaidura (1855) is at best a superspecies, and merger into Zenaida (1838) follows Goodwin (1958) and Merz (1963). Bond (1950) and others have indicated that South American auriculata is a geographical representative of macroura. Short, who has had field experience with auriculata and has kept graysoni (Socorro Island, Mexico) in captivity, considers them very closely related, possibly conspecific. Racial variation in Z. macroura was discussed in Aldrich and Duvall (1958).
- DA 7. Columbina passerina. The genus Columbigallina (1826) is merged in Columbina (1825) by various authors (see R. F. Johnston, 1961). C. minuta appears to be related to passerina.
- DA 8. Columbina squammata. "Scardafella" (1855) is merged into Columbina following R. F. Johnston (1961). We agree with the merger of inca, formerly considered a separate species, into C. squammata (South America) by Hellmayr and Conover (1942).
- DA 9. Leptotila verreauxi. The decipiens group (South America) may comprise a separate species forming a superspecies with verreauxi (see Meyer de Schauensee, 1966), but is here treated as conspecific with the latter.
- DC 1. Coccyzus minor. C. ferrugineus of Cocos Island is closely related to C. minor (Meyer de Schauensee, 1966) and is probably conspecific, but perhaps a separate species. C. minor may form a superspecies with South American C. melacoryphus (Short, pers. observ.).
- DC 2. Coccyzus [americanus]. C. euleri of South America is a close relative of C. americanus, possibly even conspecific with it.
- EA 1. Tyto [alba]. Continental populations of this cosmopolitan owl pose no taxonomic problems, but insular allopatric forms offer some difficulties. T. rosenbergii (Celebes; see Stresemann, 1940) is presumably a member of the same superspecies as alba. The West Indian glaucops group (insularis, glaucops, and nigrescens) of dark-colored races is distinctive.
- EB 1. Otus asio. Marshall (1967) has demonstrated that O. asio is comprised of four morphologically and vocally well-defined taxa, asio, kennicottii, seductus, and cooperi. These largely allopatric forms, each polytypic, may be incipient species or components of a superspecies. Mexican seductus and cooperi are entirely allopatric but asio and kennicottii meet in several places (e.g., Arkansas River, Big Bend of Rio Grande) in the southern Great Plains region. There opportunity for contact is ecologically limited, and mixed pairs and pairs of both phenotypically pure parental forms were encountered. Marshall (1967) reviewed most

of the races, and Miller and Miller (1951) discussed the taxonomy of screech owls of the arid Southwest. Mention might be made of Owen's (1963) bizarre treatment, which recognizes no subspecies of *O. asio!* Marshall (1966) has shown that *Otus bakkamoena* of eastern Asia, previously considered either conspecific with *O. asio* (Deignan, 1950) or at least closely related (Vaurie, 1965a), is not at all closely related to *asio*. (See EB 2.)

- EB 2. Otus trichopsis. This screech owl is related to O. asio through the kennicottii group of that species (Marshall, 1967).
- EB 3. Otus [scops]. Otus flammeolus is closely related to O. scops of Eurasia and comprises a superspecies with it. According to Marshall (1966) the two forms are not conspecific; he considered them to comprise a superspecies. O. brucei (Near East to central Asia) is very closely related to these species (Voous, 1960) but is sympatric with O. scops over a wide area (Vaurie, 1965a), hence does not comprise part of this superspecies.
- EB 4. Bubo [bubo]. We consider bubo, virginianus, and africanus closely related but not conspecific (see Voous, 1960); indeed it is not entirely clear whether they comprise a superspecies or a species group. A hybrid of B. bubo × B. virginianus has been produced in captivity (Gray, 1958). Races of Middle and South American forms of virginianus were reviewed by Traylor (1958) and by Webster and Orr (1958), and some North American races were discussed by Taverner (1942) and Snyder (1961). The South American nacurutu and nigrescens are distinctive races of B. virginianus.
- EB 7. Glaucidium [gnoma]. This variable species appears very closely related to the Cuban siju. Racial differentiation is considerable, with G. g. pinicola and G. g. gnoma differing in vocalizations and habitat preference in Arizona (Phillips, in Phillips, et al., 1964). Along with the superspecies G. [brasilianum] and G. minutissimum (Neotropics), and possibly the African G. perlatum, this superspecies forms a well-defined group within the genus. (See EB 8.)
- EB 8. Glaucidium [brasilianum]. Glaucidium nanum (South America) is very closely allied with G. brasilianum (Short, field obser.), and may be conspecific (Meyer de Schauensee, 1966). It is here included within this superspecies along with the highland Middle American and South American G. jardinii, which may be but an altitudinal form of brasilianum (Meyer de Schauensee, 1966). (G. jardinii could conceivably prove to be instead the southern montane representative of G. gnoma). Phillips (1966) most recently discussed variation in brasilianum. (See EB 7.)
- EB 9. Micrathene whitneyi. Distinctive M. w. graysoni of Socorro Island, Mexico, is considered conspecific by most authors.
  - EB 10. Athene cunicularia. We agree with the merger of Speotyto

- (1842) into Athene (1822), and the relationship of cunicularia with A. noctua of Eurasia suggested by Meinertzhagen and Voous (in Voous, 1960). Distinctive races include nanodes (coastal Peru), cunicularia (southern South America), and brachyptera (northern Venezuela).
- EB 11. Strix [varia]. Included with S. varia is the Middle American S. v. fulvescens, sometimes considered a separate species (Eisenmann, 1955). J. T. Marshall, Jr. informs us (pers. comm.) that vocalizations of fulvescens are the same as those of varia. S. varia and S. occidentalis are closely related, allopatric forms that apparently comprise a superspecies. The relationship of the American group to Eurasian S. uralensis and S. aluco is not clear, but it appears that neither is sufficiently close to the superspecies varia to be included therein. S. uralensis is probably somewhat closer to the varia group than is S. aluco, which seems to us not as closely related to uralensis as Voous (1960) implied. Conceivably South American S. rufipes and S. hylophila are nearer [varia] than are Old World species.
- EB 12. Strix nebulosa. This species is not as closely related to the species discussed in EB 11 as the latter are among themselves.
- EB 13. Asio otus. A number of long-eared owls (abyssinicus of Africa, clamator and stygius of the Neotropics, and madagascarensis) are related to A. otus and may comprise a superspecies or a species group with it. J. T. Marshall, Jr. (pers. comm.) considers "Rhinoptynx" clamator an Asio and probably a geographical representative of A. otus, as did Voous (1960). Wetmore (pers. comm.), following Marshall, believes clamator may be intermediate between A. otus and A. flammeus. A. abyssinicus was considered a geographical representative of A. otus by Voous (1960), while White (1965) treated them as conspecific. A. stygius and A. madagascarensis also appear closely related to A. otus, but the nature of their relationship remains to be elucidated. Races of North American forms were discussed briefly by Godfrey (1948).
- EB 14. Asio flammeus. A. capensis (Africa) seems closely related to A. flammeus (Voous, 1960).
- EB 16. Aegolius [acadicus]. Marshall (1943) has shown that Central American A. ridgwayi has an adult plumage resembling the immature plumage of A. acadicus; their vocalizations are similar. These are treated as components of the superspecies but they may instead comprise a single polytypic species. The South American A. harrisii is "immature-plumaged" as well, but other differences suggest that it is more distantly related to A. [acadicus].
- EC 1. Caprimulgus [carolinensis]. The vocalizations and life histories of various species in this difficult genus are insufficiently known. Bond (1950) has considered South American and Middle American C. rufus a geographical representative of carolinensis.
  - EC 2. Caprimulgus [vociferus]. Rare noctitherus of Puerto Rico is

now held by Wetmore (1962) to be a separate species, but it is nevertheless very closely related to *C. vociferus*.

- EC 3. Phalaenoptilus nuttallii. The most recent revision of some North American forms is that of van Rossem (1941).
- EC 5. Chordeiles minor. West Indian nighthawks vicinus and gundlachii, usually treated as races of C. minor, have quite different vocalizations (Bond, 1950) and they may be reproductively isolated from North American C. minor (Nicholson, 1957; Sutherland, 1963), but will need further study to clarify the issue. C. minor and C. acutipennis are closely related, generally allopatric (ecologically separate) species, which are morphologically convergent in Middle America (Eisenmann, 1963). Various races of C. minor have recently been discussed by Selander (1954) and by Eisenmann (1962c).
- ED 1. Cypseloides [niger]. The genera of chaeturine swifts are unclear (Lack, 1956; Orr, 1963). Eisenmann and Lehmann's (1962) recently described C. lemosi (Colombia) seems quite closely related to niger, if not conspecific with it. They are treated here as comprising a superspecies. South American rothschildi and fumigatus may belong to this superspecies as well (Short, pers. observ.).
- ED 2. Chaetura [pelagica]. C. pelagica, C. vauxi, and C. chapmani are very colsely related allopatric taxa, but are probably not conspecific (Lack, 1956; Wetmore, 1957). Various southern forms of vauxi were discussed by Sutton and Phelps (1948), while Phillips (1966) treated Mexican populations. Included in C. vauxi is the Middle American richmondi group which includes the Venezuelan form aphanes, possibly a separate species.
- EE 1-11. Hummingbird genera. The genera of hummingbirds pose one of the most difficult problems in avian taxonomy (see Peters, 1945). Merging of a number of genera may be necessary (Short and Phillips, 1966). Here we merge Calypte (1856) into Archilochus (1854), but retain other genera pending studies of Central and South American relatives of the North American forms. Selasphorus, Stellula, and Archilochus may be congeneric with Mellisuga (1760). Hybrids involving these genera are of A. alexandri × A. costae (two specimens) and A. alexandri × A. anna, intragenerically; intergeneric hybrids are of A. alexandri × Selasphorus playtcercus, A. anna × S. sasin (four individuals), A. anna × Stellula calliope, A. costae × Stellula calliope, Stellula calliope × Selasphorus rufus, and A. costae × Selasphorus platycercus (Banks and Johnson, 1961; Short and Phillips, 1966). It would be premature to lump all these genera until a study is made of the tropical species (Selasphorus and Mellisuga).
- EE 1. Archilochus [colubris]. Archilochus colubris and A. alexandri are very closely related, geographic representatives. They are strictly allopatric as far as is known, but they may meet during the breeding season in the southern Plains (the two occur near Oklahoma City; one

possible hybrid male was noted by Vacin, 1969). A. costae, considered congeneric following Phillips, et al. (1964), is a close relative of this superspecies, and it particularly resembles A. alexandri (females virtually identical, Short and Phillips, 1966). These are considered as comprising a species group.

- EE 2. Archilochus costae. (See EE 1.)
- EE 3. Archilochus anna. This species may be more closely allied to Selasphorus [rufus] than to other species of Archilochus. (See also EE 8.)
- EE 4. Selasphorus platycercus. May be more closely related to Archilochus [colubris] than to other North American species of Selasphorus. We retain the genus Selasphorus because of the dearth of knowledge of Central American species of this genus, but clearly it is very closely related to, if not congeneric with, Archilochus.
- EE 5. Selasphorus [rufus]. S. rufus and S. sasin are closely related forms which appear to have mutually exclusive breeding ranges (Grinnell and Miller, 1944). We consider them to constitute a superspecies. (See also EE 3.)
- EE 6. Stellula calliope. The species is closely related to, and probably congeneric with, Archilochus and Selasphorus.
- EE 7. Eugenes fulgens. Middle American spectabilis is a well-differentiated form (Eisenmann, 1955) here considered conspecific with fulgens. (See also EE 11.)
- EE 8. Lampornis clemenciae. The race bessophilus is weakly defined (paler than clemenciae; Oberholser, 1918b). A recently collected (Russell, unpubl.) hybrid of L. clemenciae  $\times$  Archilochus costae (or possibly A. anna) has been seen by Short.
- EE 9. Amazilia [rutila]. Amazilia yucatanensis and Middle American A. rutila are possibly conspecific geographical representatives, here considered to comprise a superspecies. A. tzacatl is a closely related species that replaces A. yucatanensis in wetter regions (Blake, 1953).
- EE 10. Hylocharis [leucotis]. H. xantusii is a relict form closely related to H. leucotis and endemic to southern Baja California (the most strongly differentiated avian form in that region; Short, 1965a). It is here considered a species comprising a superspecies with leucotis.
- EE 11. Cynanthus latirostris. Cynanthus, closely related to Amazilia, is comprised of two species, C. latirostris and C. sordidus, which have hybridized in Mexico, (Friedmann, et al., 1950). We do not consider them as comprising a superspecies because several little-known, but well-differentiated, races (especially doubledayi and lawrencei of C. latirostir could prove specifically distinct. C. latirostris has hybridized also with Amazilia violiceps (Gray, 1958) and with Eugenes fulgens (Short and Phillips, 1966).
- EG 1. Ceryle alcyon. C. torquata appears to be a close relative of C. alcyon. Races of alcyon are weakly defined (Todd, 1963; Short, unpubl.). We follow Peters' (1945) merger of Megaceryle into Ceryle.

- EG 2. Chloroceryle americana. C. americana appears closely related to C. amazona. Van Rossem and Hachisuka (1938) discussed races of americana.
- EH 1. Picoides [scalaris]. Recent studies by Short (1969a, in press, b) have shown that scalaris and nuttallii are closely related, essentially allopatric species that hybridize regularly but sporadically where they meet. Their ranges are mutually exclusive in California, but there exists a small area of overlap and hybridization in northern Baja California (hybrids comprise about 10% of the population there). These species comprise a superspecies very closely related to P. pubescens. P. nuttallii is sympatric with P. pubescens in California, but at the southern limit of its range pubescens is replaced in its preferred habitat (riparian woodland) by nuttallii; here the two hybridze (rarely), probably as a result of the scarcity of P. pubescens where individuals of P. nuttallii are plentiful. Among North American species of Picoides, P. scalaris is probably closest to the ancestral species that gave rise to this group. Its races are well marked, especially the eremicus-lucasanus group (Baja California; Short, 1968a), and parvus of Yucatán. For a discussion of its races see Oberholser (1911b) and Short (1968a). The genera and arrangement of woodpeckers used herein are those proposed by Bock and Short (MS). Dendrocopos (1816) is merged in Picoides (1799) following Delacour (1951) and Bock and Short (MS).
- EH 2. *Picoides pubescens*. The Downy Woodpecker is related not to the superficially similar *P. villosus*, but instead to the superspecies *P. [scalaris*], which see. Races of *pubescens* are much less diverse than are those of *villosus* (see Burleigh, 1960b; Todd, 1963; and Mengel, 1965, for recent information on subspecies of *P. pubescens*).
- EH 3. *Picoides borealis*. This species appears related to *P*. [scalaris], but it is quite distinct. The subspecies of borealis were discussed by Wetmore (1941).
- EH 4. Picoides stricklandi. We follow J. Davis (1965) in considering arizonae conspecific with stricklandi, rather than maintaining both as separate species (of one superspecies). Its closest relative among modern species of Picoides is villosus (Short, in press, b). J. Davis (1965) discussed the races of this species.
- EH 5. Picoides villosus. Races of villosus were treated by Oberholser (1911a). There is marked variation among these races, with Queen Charlotte Islands picoideus, Bahama Islands piger and maynardi, and extimus of southern Central America being the most distinctive. The New World species of Picoides comprise a monophyletic group of species (Short, in press, b; Goodwin, 1968), contra Voous (1947). All of these species are closely related, with P. stricklandi perhaps the closest relative of villosus. One hybrid is known (Miller, 1955) of P. villosus X P. scalaris.
  - EH 6. Picoides albolarvatus. This superficially very distinct species

is probably a rather close relative of *P. villosus* and *P. sticklandi*; some of its vocalizations resemble those of *P. nuttallii* (Short, in press, b). Its two subspecies are weakly characterized.

EH 7. Picoides arcticus. Short (in press, b) agrees with Goodwin (1968) that the three-toed woodpeckers are closely related to North American species of Picoides, especially P. villosus. (See also EH 1.)

- EH 8. Picoides tridactylus. Todd (1963) discussed North American races of this species, while Vaurie (1965a), characterized the Palearctic forms. The latter author considers funebris (eastern Asia) a very distinct subspecies. The two species of three-toed woodpeckers comprise a species group.
- EH 9. Melanerpes formicivorus. This species forms a species group with M. erythrocephalus (see EH 10). The South American race flavigula is strongly marked in several ways; for example, males have the head pattern of females of other races and females lack bright color on the head. A shift in such pattern involving sexual recognition is significant in woodpeckers (Short, per. observ.).
- EH 10. Melanerpes erythrocephalus. The Red-headed Woodpecker is related to the western Acorn Woodpecker (M. formicivorus) in the same way as are the jays Cyanocitta cristata and C. stelleri and the bluebirds Sialia sialis and S. mexicana. That is, they are closely related but comprise a species group, not a superspecies, for their divergence occurred long ago. M. e. caurinus is a poorly defined race (Brodkorb, 1936).
- EH 11. Melanerpes [carolinus]. The Centurus group of Melanerpes is mainly comprised of allopatric forms, many of which appear to be geographical representatives. Selander and Giller (1959, 1963) have provided information elucidating many of their interrelationships, but others remain to be demonstrated. M. aurifrons, carolinus, hoffmanni, superciliaris, and uropygialis are morphologically rather similar geographic representatives, here treated as comprising a superspecies. M. hoffmanni of southern Middle America was considered a geographical representative of aurifrons by Selander and Giller (1963); it is possibly conspecific with aurifrons. The allopatric West Indian superciliaris is distinct, but an obvious derivative of carolinus (Selander and Giller, 1963; Bock and Short, MS). M. aurifrons and M. carolinus meet and overlap by a few miles in Texas, apparently without interbreeding (Selander and Giller, 1959). M. uropygialis, far from being conspecific with M. hypopolius (Middle America; latter related instead to M. chrysogenys), is a geographic representative of aurifrons and carolinus, and it hybridizes with aurifrons where these meet in Mexico (5% of birds taken in two areas of contact are hybrids according to Selander and Giller, 1963). M. rubricapillus is related to this superspecies, but is a distinct species for its close relative M. pygmaeus is sympatric with M. aurifrons dubius in Yucatan. We tentatively place pygmaeus and rubricapillus in a species group with M. [carolinus]. The races of M. carolinus were discussed in Burleigh and Lowery (1944)

and by Koelz (1954), while Selander and Giller (1963) reviewed subspecies of *M. aurifrons*. Among races of the latter, *dubius*, *polygrammus* of southern Mexico, and *santacruzi* of Mexico to Nicaragua are distinctive and were once considered separate species. We follow Peters (1948), Goodwin (1968), and others in merging *Centurus* in *Melanerpes* for the reason noted by Meyer de Schauensee (1966), namely that the "*Tripsurus*" forms (and "*Trichopicus*," Short, 1970) bridge the two groups making it impossible to separate the continuum.

EH 12. Melanerpes lewis. This peculiar species is not generically separable from Melanerpes (Bock and Short, MS).

EH 13. Sphyrapicus [varius]. Short (1969a) recognized three species comprising this superspecies, S. varius, S. nuchalis, and S. ruber. Although Howell (1952; followed by the A. O. U. Check-list, 1957) considered them conspecific, only very limited interbreeding occurs where they meet. S. ruber hybridizes only sporadically with S. varius, although the two overlap in British Columbia (Howell, 1952; Dickinson, 1953). Several winter-taken hybrids of S. varius and S. nuchalis are known. It is not clear to what extent they meet in Alberta, and there is no evidence that they freely interbreed. S. ruber and S. nuchalis hybridize in a small zone of overlap in California, but hybrids are not numerous. The available evidence is indicative of restricted interbreeding, warranting specific status of these taxa. Howell (1953) discussed races of these species and Ganier (1954) has since described another race of S. varius. S. thyroideus is considered closely related to S. [varius]. It has hybridized twice with S. [varius] nuchalis (Short and Morony, in press).

EH 15. Colaptes auratus. Colaptes auratus is comprised of five morphologically divergent taxa (subspecies groups), three of which, namely the auratus, cafer, and chrysoides groups, are North American (Short, 1965a). The other two groups, the Cuban-Grand Cayman chrysocaulosus group (Short, 1965b) and the Central American mexicanoides group (Short, 1967a) are entirely allopatric, but the North American groups occupy contiguous ranges and hybridize wherever they are in contact. The eastern auratus and wester cafer groups are connected, as well as separated, by a vast entirely hybrid population; their interbreeding results in widespread introgression (Short, 1965a). The chrysoides group is largely separated from cafer by unfavorable habitat but they interbreed wherever they meet. Geographically isolated, partly stabilized hybrid swarms mark former sites of contact between the parental forms (Short 1965a; Short and Banks, 1965). Although they are generally considered as separate species, the application of biological species criteria demands their conspecificity. Each of the three groups is itself polytypic. This situation somewhat resembles that of the Screech Owls (Otus asio) except that interbreeding between the subspecies is massive rather than restricted.

EH 16. Dryocopus pileatus. D. pileatus is most closely allied to Neotropical D. lineatus (Short, 1965c), although it is also fairly closely related

- to Old World forms martius and javensis (contra Goodwin, 1968). The races of pileatus are moderately differentiated, although they exhibit rather striking size differences (Short, unpubl.).
- EH 17. Campephilus [principalis]. Short (in press, a) considers closely related principalis and imperialis (Mexico) as elements of a single superspecies. These are related not to Patagonian C. magellanicus, but to the Neotropical "ivory-billed" woodpeckers (Phloeoceastes) which are merged in Campephilus by Short (in press, a), as well as by Wetmore (1968). Cuban C. p. bairdi is a weakly differentiated subspecies.
- FA 1. Platypsaris [minor]. The genus Platypsaris consists of a number of essentially allopatric taxa. Of these, minor (northern South America), homochrous (Panama, northwestern South America), and aglaiae are treated here as species comprising a superspecies, while P. niger (Jamaica) and P. rufus (central South America) are considered to comprise a species group with the superspecies minor. If Meyer de Schauensee (1966) is correct in treating the first group as conspecific, then rufus and niger would comprise a superspecies with minor. Platypsaris may be congeneric with Pachyramphus (Bond, 1967).
- FB 1. Tyrannus tyrannus. The genus Tyrannus is the subject of a recent critical appraisal by W. Smith (1966). Short is not fully convinced that this species is particularly close to any of the other kingbirds, but we follow Smith in placing tyrannus near dominicensis.
- FB 2. Tyrannus dominicensis. The West Indian species of Tyrannus (dominicensis, cubensis, and caudifasciatus) comprise a species group (W. Smith, 1966), possibly closely related to T. tyrannus. The recently described races of this species (Brodkorb, 1950) have not been generally accepted.
- FB 3. Tyrannus [melancholicus]. W. Smith's (1966) studies indicate that two populations, couchii and the melancholicus group, differ strikingly in the whole repertoire of their vocalizations and appear to represent (sibling) species. It is not altogether clear what transpires in the region of contact in southern Mexico. We provisionally treat them as species within a superspecies. T. niveigularis (northwestern South America) and T. albigularis (northern South America), and the superspecies melancholicus comprise a species group of kingbirds according to Smith (1966).
- FB 4. Tyrannus verticalis. This monotypic kingbird seems closely related to vociferans. W. Smith (1966) considered it to comprise a "western" group of species with vociferans and crassirostris. We follow Smith in recognizing this species group.
- FB 5. Tyrannus vociferans. Races of this kingbird are not strongly differentiated. (See also FB 4.)
- FB 6. Tyrannus crassirostris. This kingbird has only recently entered the United States, breeding now in the southeastern Arizona-southwestern

- New Mexico region (see Phillips, et al., 1964). It is generally considered to be monotypic. (See also FB 4.)
- FB 7. Tyrannus forficatus. The Scissor-tail Flycatcher is included within Tyrannus, following W. Smith (1966).
- FB 9. Myiodynastes luteiventris. M. maculatus (Middle and South America) is closely related to M. luteiventris, the two being sibling species (Monroe, 1968). Races of luteiventris are weakly differentiated and the species may be monotypic as Monroe (1968) suggested.
- FB 10. Myiarchus [crinitus]. Myiarchus tyrannulus and M. crinitus are very closely related flycatchers that replace each other geographically (Lanyon, pers. comm.). They are considered to comprise a superspecies. Races of tyrannulus were discussed by Lanyon (1960b); brachyurus of Nicaragua and Costa Rica is distinctive. We concur with Phillips (in Phillips, et al., 1964) that boreus is a synonym of crinitus; M. crinitus is hence monotypic. Lanyon has yet to complete his studies of South American Myiarchus and species groups within the genus cannot yet be designated with certainty.
- FB 11. Myiarchus [cinerascens]. The relationship of M. cinerascens with Middle American M. nuttingi has been discussed by Lanyon (1961). We treat these species as comprising a superspecies, but their relationships may not be quite that close (Lanyon, pers. comm.). Some earlier authors considered them conspecific. Races of cinerascens were discussed by Lanyon (1963).
- FB 13. Sayornis phoebe. The Phoebe and Black Phoebe (Sayornis nigricans) appear more closely related to each other than either is to saya, although we do not consider them very closely allied. Like the bluebirds (Sialia) and blue jays (Cyanocitta) these species may represent an ancient east-west species pair (Short, unpubl.).
- FB 18. Empidonax [traillii]. The investigations of Stein (1958, 1963) indicate that traillii and alnorum are largely allopatric but partly sympatric sibling species. We are not convinced that hybridization does not occur, and teel that at this stage of our knowledge they are best considered species comprising a superspecies. Use of E. alnorum as the specific name for one taxon follows studies by Eisenmann (unpubl.). We consider these species monotypic in view of their variability and difficulties in determining the specific, let alone subspecies, status of individual birds. Various races have been discussed by Phillips (1948), Aldrich (1951), Snyder (1953), and Parkes (1954). The rather close relationship of Empidonax and Contopus is suggested by a hybrid of Contopus sordidulus × Empidonax traillii (Short and Burleigh, 1965).
- FB 19. Empidonax [minimus]. We follow Johnson (1963, 1966b) in regarding the sibling species minimus and hammondii, both monotypic and endemic, as geographical representatives and components of a superspecies. Their ranges appear to overlap in western Montana and Alberta, but there is no information on their interactions. Overlap occurs in south-

central British Columbia, with no apparent interbreeding (Johnson, 1966b).

- FB 20-21. Empidonax oberholseri and E. wrightii. These sibling species seem closely related (Johnson, 1963, 1966a).
- FB 22. Empidonax difficilis. Subspecies of difficilis have been discussed by Phillips (in Phillips, et al., 1964; Phillips, 1966), who provided evidence for the recognition of flavescens (Middle America) as a race of difficilis; flavescens is usually considered a separate species. Within North America there is a possibility that the eastern hellmayri is a sibling species (Johnson, pers. comm.). Relationships of difficilis with other Empidonax are unclear.
- FB 23. Empidonax fulvifrons. Phillips (in Phillips, et al., 1964) noted the relationship of E. atriceps to fulvifrons. The species fulvifrons seems clearly to be an Empidonax; thus Brodkorb's (1936) removal of fulvifrons from Empidonax (into monotypic Cnemonax) is not supported.
- FB 24. Contopus borealis. We concur with Phillips (in Phillips, et al., 1964) that this species does not comprise a monotypic genus (Nuttallornis [1887]), but is indeed a Contopus (1855), closely related to the fumigatus group. We note that borealis and pertinax occupy mutually exclusive ranges, although they may meet in the White Mountains of Arizona (Phillips, et al., 1964).
- FB 25. Contopus [fumigatus]. Zimmer (1939) merged Middle American lugubris and pertinax with South American fumigatus, and he is followed by various authors, recently including Meyer de Schauensee (1966). We recognize that these may be conspecific, but prefer at present to treat them as comprising a superspecies, pending studies of their habits and vocalizations. There is no modern review of the races of pertinax, which has hybridized with C. sordidulus (Phillips and Short, 1968).
- FB 26. Contopus [virens]. The pewees C. virens and C. sordidulus pose a difficult taxonomic problem because of their great similarity in morphology. Several recent workers (Aldrich, in Jewett, et al., 1953; Meyer de Schauensee, 1966) consider them conspecific. Hybridization occurs at least sporadically where they make contact in the Great Plains (Barlow and Rising, 1965; Short, unpubl.), and possibly in Manitoba. Because of post-mortem color changes (diminution of yellow; enhancement of brown), older specimens of the two are less alike than are recently taken specimens. We tentatively consider them as semispecies of a superspecies; they are sibling species as well. Racial splitting of sordidulus by Burleigh (1960a) is unwarranted, especially considering that dates represented by some his critical specimens are well within the migration period. There are probably only three recognizable races of sordidulus, namely sordidulus (Mexico to Panama), peninsularis (Baja California), and veliei (western North America). Phillips and Parkes (1955) discussed some of these races. We are not certain of the interrelationships among pewees, as this superspecies may be closely related either to the

West Indian "Blacicus" group or to the tropical pewee (cinereus) complex. A hybrid is known of C. sordidulus X C. pertinax (Phillips and Short, 1968), as well as of C. sordidulus X Empidonax traillii (Short and Burleigh, 1965).

- FB 27. Pyrocephalus rubinus. This flycatcher is in need of a taxonomic review in its entirety. Very distinct subspecies include nanus (Galapagos), saturatus (northeastern South America), and obscurus (northwestern South America); the latter has a melanic phase ("obscurus" phase), once considered specifically distinct (Cory and Hellmayr, 1927). Howell (1965) recently discussed the Middle American races.
- FB 28. Camptostoma [obsoletum]. The small "beardless" flycatchers, C. obsoletum (southern Middle America, South America) and C. imberbe, are largely allopatric. They meet and barely overlap in Costa Rica (Slud, 1964). They are treated here as comprising a superspecies.
- GA 1. Eremophila [alpestris]. This cosmopolitan group is comprised of E. alpestris and the North African desert form bilopha, shown to be specifically distinct by Stresemann (1926) and so considered by Vaurie (1954b). E. bilopha appears to be more distinctive than any of a number of groups (see Vaurie, 1954b) of the strongly polytypic species alpestris. We consider bilopha and alpestris to comprise a superspecies. The two apparently are ecologically separated in Africa. Other authors (e.g., Hartert, 1927; Voous, 1960) consider bilopha conspecific with alpestris. The races of Horned Lark are in need of a thorough, world-wide review. Old World races were discussed by Vaurie (1951a, 1954b), and the western North American forms by Behle (1942) and by Phillips (in Phillips, et al., 1964).
- GB 1. Tachycineta thalassina. Iridoprocne (1878) is merged into Tachycineta (1851) following Mayr and Greenway (1960). Races of thalassina are moderately differentiated.
- GB 3. Progne [subis]. We treat P. subis, P. chalybea (Mexico to South America), P. modesta (South America), and P. dominicensis (Middle America, West Indies) as species comprising a superspecies, following Mayr and Greenway (1960) and Meyer de Schauensee (1966). One or more of these may prove conspecific with subis. Studies are needed in the areas of contact, such as Mexico and central Argentina (where modesta and chalybea hybridize; Eisenmann, pers. comm., and see Meyer de Schauensee, 1966), to determine interactions of these closely allied forms. Eisenmann (1959) discussed their relationships. Races of subis were discussed by Phillips (in Phillips, et al., 1964), by Johnston (1966), and by Behle (1968). Following Mayr and Bond (1943) we place this martin near Tachycineta.
- GB 4. Riparia riparia. Eurasian races of this swallow were reviewed by Vaurie (1951b). R. congica of the Congo River is allopatric and occasionally has been merged into riparia. These may comprise a superspecies, but in view of the sympatry (without interbreeding) of riparia

- and the equally similar *paludicola* in Africa and India (Voous, 1960), and the sympatric occurrence of several species of this genus in southern Africa, it seems best to place *congica* within a species group with *riparia* and the related *paludicola*.
- GB 5. Stelgidopteryx ruficollis. Brodkorb (1942) and Phillips (in Phillips, et al., 1964) discuss variation in this swallow. Its relationships are uncertain.
- GB 6. Hirundo [rustica]. The swallows H. rustica, H. tahitica (southeast Asia, Australia, and southwest Pacific), H. angolensis (eastern, southern Africa), and H. lucida (western, northern Africa) are allopatric, related species that comprise a superspecies. There is slight overlap in Formosa between rustica and tahitica (Voous, 1960). The superspecies rustica comprises a species group with aethiopica, albigularis, and smithii, and possibly other species of Hirundo. Variation of Eurasian races of rustica is discussed in Vaurie (1951b, 1954c); H. r. savignii (Egypt), tytleri (Siberia), and North American erythrogaster (once considered a separate species) are morphologically distinctive.
- GB 7. Petrochelidon [fulva]. The Cliff Swallow (pyrrhonota) and Cave Swallow (fulva) are largely allopatric, related species that narrowly overlap without interbreeding in Texas (Selander and Baker, 1957). They appear to comprise a superspecies. Races of pyrrhonota were discussed by Phillips (in Phillips, et al., 1964). P. fulva occupies a fragmented range; South American forms (the ruficollaris group) are distinctive and have been considered a separate species (Meyer de Schauensee, 1966). Relationships among species of Petrochelidon are uncertain.
- GC 1. Perisoreus [infaustus]. Until Aldrich (1943) demonstrated intergradation between the obscurus and canadensis racial groups, these were considered separate species; they are now treated as conspecific. Todd (1963) discussed variation in eastern races of P. canadensis and Aldrich (1943) and Miller (1950) discussed some western races. The genus Perisoreus comprises a superspecies with the species infaustus (northern Eurasia), internigrans (montane northwest China), and canadensis replacing each other geographically.
- GC 2. Cyanocitta cristata. The eastern Blue Jay probably evolved from a common ancestor with C. stelleri early in the history of New World jays. These species, although not very closely related, comprise an ancient species group. Several hybrids of stelleri × cristata have recently been found near Boulder, Colorado (J. W. Hardy, pers. comm.). The races of cristata are not strongly differentiated. Bond's (1962) race burleighi is not distinguishable from bromia. Mengel (1965) discussed certain of the races of cristata.
- GC 3. Cyanocitta stelleri. Studies are needed of the hybridization reported (Moore, 1954; Brown, 1963) between black-crested (azteca group) and blue-crested (coronata group) forms in Mexico. These forms differ in a number of ways, as Brown (1963) has shown. Western races

were reviewed by Stevenson (1934) and by Phillips (in Phillips, et al., 1964), while Moore (1954) discussed the Mexican races. (See also GC 2.)

- GC 4. Aphelocoma coerulescens. Pitelka (1951b) reviewed races of this species, and the relationship between the californica group and the well-differentiated, disjunct Florida race coerulescens, long considered a distinct species. Two moderately differentiated western groups, the californica and woodhousei groups, interbreed in the western Great Basin region.
- GC 5. Aphelocoma ultramarina. Pitelka (1951b) reviewed races of ultramarina.
- GC 6. Cyanocorax yncas. The Green Jay, the northernmost outlying species of this Neotropical genus, was formerly separated generically (Xanthoura). The species of Cyanocorax are currently being investigated by several workers. The northern luxuosus group of races was once considered a separate species. Zimmer (1953) discussed variation in some southern races.
- GC 7. Pica [pica]. Vaurie (1954a) has discussed the Palearctic races of P. pica. Californian nuttalli is allopatric, and the most distinct magpie; nevertheless, it may be conspecific with pica, as it was considered by Amadon (1944). The two approach within 80 miles of one another in California (Grinnell, et al., 1930). We tentatively maintain nuttalli as a species comprising a superspecies with pica.
- GC 8. Corvus [corax]. The ravens C. corax and C. ruficollis (northern Africa to west central Asia) appear to be geographic representatives. They apparently overlap without interbreeding in southwestern Asia (Vaurie, 1954a). Eurasian races of corax were discussed by Vaurie (1954a) while Oberholser (1918a) last reviewed New World races. The Hawaiian Raven (C. tropicus) and North American C. cryptoleucus appear to be derivatives of early corax stock; they comprise a species group with the superspecies C. corax.
  - GC 9. Corvus cryptoleucus. (See GC 8.)
- GC 10. Corvus [brachyrhynchos]. The North American Common Crow has been considered conspecific with Eurasian C. corone by some authors, but its vocalization is very different and it appears closer to other New World crows. Perhaps it is nearest the ancestral form from which other American crows evolved, and hence stands between them and the Old World crows. It seems prudent to consider the New World crows as a species group, including the brachyrhnchos group, the ossifragus group, leucognaphalus (Hispaniola and Puerto Rico), and jamaicensis (Jamaica). The entire group is the subject of a monograph by D. W. Johnston (1961). The northwestern race caurinus is sometimes considered a separate species, but as it appears to intergrade with brachyrhynchos (D. W. Johnston, 1961), it is believed to be conspecific. Following Johnston, Cuban nasicus is thought to be closely related, comprising a superspecies with brachyrhynchos; leucognaphalus may also be

as closely related, as it has been considered conspecific with nasicus (see Bond, 1956).

- GC 11. Corvus [ossifragus]. The Fish Crow appears closely related to C. imparatus (Mexico) and to C. palmarum (Cuba, Hispaniola); they are here treated as comprising a superspecies (see D. W. Johnston, 1961). (See also GC 10.)
- GC 12. Gymnorhinus cyanocephalus. The relationships of this peculiar species remain obscure (Amadon, 1944).
- GC 13. Nucifraga columbiana. This nutcracker is related to Palearctic caryocatactes, but the relationship is probably not close. Mayr (persobserv.) notes that their vocalizations are similar. They are treated as components of a species group.
- GD 1. Parus [atricapillus]. Relationships of P. atricapillus and P. carolinensis remain unclear despite the studies of Tanner (1952), Brewer (1963), and Rising (1968). They hybridize in some places (e.g., Kansas, Illinois and New Jersey), at least to a limited degree. Duvall (1945a) and Behle (1951) discussed races of atricapillus and Lunk (1952) reviewed P. carolinensis. Mayr (1956), Snow (1956), and Vaurie (1957b) have recently presented arguments against conspecificity of Parus montanus (Eurasia) and P. atricapillus, which have often been merged. Although they are probably specifically distinct, Short remains to be convinced because: 1) atricapillus appears to be a reentrant into North America, therefore requiring an Old World related form; and, 2) the vocal differences between montanus and atricapillus may reflect the fact that each is sympatric with a different array of parids, and not necessarily that they are specifically distinct. We treat montanus, atricapillus, and carolinensis as component species of a superspecies. (See also GD 2 and GD 3.)
- GD 2. Parus sclateri. This chickadee is allopatric with both P. atricapillus and P. gambeli, to both of which it appears related; it may represent a southern component of the atricapillus superspecies, but at any rate these comprise a species group. Miller and Storer (1950) presented a cursory review of its subspecies.
- GD 3. Parus gambeli. The Mountain Chickadee seems related to others of the atricapillus group. Some races were discussed by Phillips (in Phillips, et al., 1964).
- GD 4. Parus [hudsonicus]. P. hudsonicus, P. cinctus, and P. rufescens appear to comprise a related group of species (Grinnell, 1904) which replace each other geographically. They are treated here as comprising a superspecies. P. cinctus, essentially a Palearctic species, meets and slightly overlaps with hudsonicus in Alaska without interbreeding (Miller, 1943). P. rufescens and hudsonicus appear to have contiguous ranges; they may meet in northern Washington (Aldrich, in Jewett, et al., 1953) and in British Columbia (Dickinson, 1953). Their intraspecific variation

has been discussed by Vaurie (1957b) for *cinctus* and by Miller (1943), Godfrey (1951), and Todd (1963) for *hudsonicus*.

- GD 5. Parus wollweberi. Relationships of this tit are not well known (Dixon, 1955) but its habits suggest that it is related to North American chickadees (Short, pers. observ.; see also Phillips' comments in Phillips, et al., 1964), and not to various crested tits of North America (P. [bi-color]) or of the Old World. Van Rossem (1947a) discussed its variation.
- GD 6. Parus [bicolor]. Dixon (1955) studied hybridization between and variation within the bicolor and atricristatus groups of P. bicolor; these groups interbreed freely in a narrow zone and hence are considered conspecific (as by Snow, 1967c, and various authors). P. inornatus is an allopatric western form closely resembling bicolor in habits and vocalizations (Short, pers. observ.). There appears to be no reason not to consider it a western representative of bicolor; we treat it as a component species of the superspecies bicolor, although it may prove more distinctive. Variation in inornatus was discussed by Miller (1946; but see also remarks of Phillips, in Phillips, et al., 1964).
- GD 7. Auriparus flaviceps. Variation in North American races is briefly discussed by Phillips (in Phillips et al., 1964). Relationships of the Verdin are unclear; various authors, including Snow (1967b), place Auriparus in the Remizidae instead of the Paridae.
- GD 8. Psaltriparus minimus. The black-eared form of bushtit, formerly known as P. melanotis, has proved to represent a morph of the plain-eared forms, and is hence considered conspecific with minimus (Raitt, 1967). Distinctive also are the plumbeus and minimus groups, once considered separate species, that hybridize in secondary contacts in California (Miller, 1946). Raitt and Miller each discuss variation among various races. Psaltriparus is now considered to belong in the Aegithalidae (Snow, 1967a); indeed, we feel that Psaltriparus and Aegithalos are very closely related.
- GE 1. Sitta carolinensis. Variation in carolinensis was discussed by Aldrich (1944b; see also Mengel, 1965). Relationships of this species are unclear. We are uncertain whether carolinensis is related to Asian leucopsis, which it somewhat resembles (Voous, 1960). The Eurasian europaea group has very different vocalizations and habits.
- GE 2. Sitta [canadensis]. We concur with Phillips (in Phillips, et al., 1964) and Greenway (1967) that S. canadensis clariterga Burleigh is not recognizable, and that canadensis is therefore monotypic. We follow Vaurie (1957c) in considering the disjunct whiteheadi (Corsica), villosa (east Asia), and canadensis related but not conspecific. The Chinese form yunnanensis appears to fall in this group also, and we consider the four forms to comprise a superspecies. Löhrl (1960, 1961) found behavioral similarities as well as differences between whiteheadi and canadensis, tending to bear out the view that they are closely related but specifically

- distinct. For a long time many authors have considered the several Palearctic forms conspecific with canadensis.
- GE 3. Sitta pusilla. Contrary to Norris' (1958) conclusion that pusilla and pygmaea are separate species, we find nothing in his analysis to indicate that they are specifically distinct. Their differences are those one would expect to find in disjunct conspecific populations inhabiting somewhat different environments. We follow Phillips (in Phillips, et al., 1964) in considering them conspecific. We note that other southeastern disjunct populations (Florida forms of Aphelocoma coerulescens and Athene cunicularia), even more geographically separated from their western relatives than is pusilla, likewise have not achieved specific distinctness. Races of pusilla were reviewed by Norris (1958). The species may represent an older invasion by ancestral canadensis stock, but this is far from certain.
- GF 1. Certhia familiaris. Various races of familiaris are discussed by Vaurie (1957d; Eurasia) and by Phillips (in Phillips, et al., 1964; western North America). The New World forms are sometimes treated as comprising a separate species (Thielcke, 1962; see also Mayr, 1956). C. brachydactyla of Eurasia is a sibling species, but has a rather different vocalization.
- GG 1. Chamaea fasciata. The Wrentit clearly seems related, although distantly, to the Old World Timaliinae (e.g., Moupinia). Certain of its races were discussed by Bowers (1960).
- GH 1. Cinclus mexicanus. Cinclus is comprised of a number of mainly allopatric, geographic representatives, but these do not form a superspecies. Their relationships are rather more distant, as suggested by the considerable overlap of C. pallasii and C. cinclus in the Himalayan area. The genus can be viewed as a species group. Among the races of C. mexicanus, ardesiaca (Middle America) appears well differentiated.
- GI 1. Troglodytes aedon. The Tropical House Wren (T. "musculus"), morphologically very similar to aedon, also resembles it in its habits and vocalization (Short, pers. observ.). We follow the various authors, including Paynter (1957a), who have merged the two forms in one species. Lanyon (1960a) demonstrated that brunneicollis and aedon hybridize freely. There remains some question (Monroe, 1968) about the interaction of the brunneicollis and musculus groups in Mexico, but, pending studies of this situation, the interbreeding of brunneicollis × aedon and the similarity of musculus and aedon dictate conspecificity of these groups. Reviews of racial variation include those of Chapman and Griscom (1924; musculus group), Oberholser (1934; aedon group), and Paynter (1957a); see also the comments of Todd (1963), Phillips (in Phillips, et al., 1964) and Mengel (1965). Holarctic T. troglodytes and the Middle and South American solstitialis group (including rufulus) are probably the nearest relatives of T. aedon.
  - GI 2. Troglodytes troglodytes. Races of this wren were discussed

- by Vaurie (1955a; Eurasian forms), by Paynter (1957a; New World races), and by Mengel (1965; New World races). Various insular (hirtensis of St. Kilda Island; pallescens of Commander Islands) and other races are strongly marked (Vaurie, 1959). The New World forms, which have been considered as comprising separate species (see Mayr, 1956), are much more restricted ecologically than are those in the Old World. (See GI 1.)
- GI 3. Thryomanes [bewickii]. Eastern races of bewickii were reviewed by Aldrich (1944a; see also Mengel, 1965). T. sissonii of Socorro Island is closely related to bewickii and is treated here as comprising a superspecies with it. They may be conspecific. Relationships within this genus are uncertain.
- GI 4. Thryothorus ludovicianus. The races of ludovicianus were reviewed by Lowery (1940) and by Godfrey (1946), but see also the remarks of Mengel (1965). The albinucha group of Middle America is often considered specifically distinct from ludovicianus. Relationships within the genus are in need of study, but closest to ludovicianus are probably the superspecies rufalbus (including nicefori and sinaloa of Middle and South America; see Paynter, 1960), modestus (Middle America), the superspecies leucotis (including superciliaris and guarayanus of Panama and South America), and longirostris (eastern Brazil).
- GI 5. Campylorhynchus [brunneicapillus]. This genus is the subject of a monograph by Selander (1964), who reviewed races of brunneicapillus in a cursory fashion. Following Selander, yucatanicus (possibly conspecific with brunneicapillus, with which it is frequently merged) and jocosus of Mexico comprise a superspecies with brunneicapillus, and this complex forms a species group with gularis (Mexico), rufinucha (Middle America), and griseus (Mexico, South America).
- GI 6. Cistothorus palustris. Races of palustris were discussed by Aldrich (1946), by Parkes (1959), and by Phillips (in Phillips, et al., 1964). Telmatodytes (1851) is merged into Cistothorus (1851; has page precedence) following Paynter (1960) and earlier authors dating back to Hellmayr (1934).
- GI 7. Cistothorus [platensis]. Races of platensis are in need of review. The South American platensis group and North American stellaris group are moderately distinct with different ecological preferences (Meyer de Schauensee, 1966); they could be specifically distinct. Very locally distributed, well-differentiated C. apolinari (near Bogotá Colombia) and C. meridae (Venezuela) are related to platensis. The former is considered a superspecies with platensis, while that superspecies and meridae comprise a species group.
- GI 8. Salpinctes mexicanus. Variation in mexicanus was considered by Aldrich (1946) and by Miller (1948). Catherpes (1858) is merged into Salpinctes (1847) following Paynter (1960).

- GI 9. Salpinctes obsoletus. Variation in the Rock Wren was discussed by Moore (1941a), by van Rossem (1943), and recently by Monroe (1968). The Central American races (guttatus, fasciatus) are strongly differentiated (Monroe, 1968).
- GK 1. Mimus polyglottos. The distinctive Middle American (and northern South American) gilvus group and magnirostris of St. Andrews Island are considered conspecific with polyglottos. These are frequently treated as separate species. Wetmore (1943) showed that gilvus and polyglottos interbreed in Mexico, and Phillips (1961) treats them as conspecific. Further study of their hybridization is necessary. Bond (1961) suggested that magnirostris and gilvus are conspecific. We follow Phillips (1961) in considering leucopterus a synonym of M. p. polyglottos. South American M. patagonicus and M. triurus, with which Short is familiar, seem among the species related to polyglottos.
- GK 2. Toxostoma [rufum]. Like Todd (1963) we question the validity of T. r. longicauda, but we tentatively recognize it. We concur with Engels (1940) that the allopatric rufum, guttatum (Cozumel Island), and longirostre comprise a superspecies.
- GK 3. Toxostoma [cinereum]. T. cinereum (Baja California) and T. bendirei are closely related as suggested by Engels (1940) and supported by field observations of both forms by Short. They are possibly conspecific, but we treat them for now as members of a superspecies. Van Rossem (1942) briefly considered variation in bendirei.
- GK 4. Toxostoma curvirostre. Races of curvirostre have been discussed by Moore (1941b) and recently by Phillips (in Phillips, et al., 1964). This thrasher is closely related to Mexican T. ocellatum, with which it is sympatric (Engels, 1940).
- GK 5. Toxostoma redivivum. Oberholser (1918e) last reviewed this thrasher. We accept the grouping of redivivum, dorsale, and lecontei in a species group following Engels (1940); redivivum and dorsale may be geographically representative species comprising a superspecies.
- GK 6. Toxostoma dorsale. Van Rossem (1946) discussed the variation of this thrasher. (See GK 5.)
- GK 7. Toxostoma lecontei. Phillips (1964) reviewed the races of lecontei. (See GK 5.)
- GK 8. Oreoscoptes montanus. Given the variation within Toxostoma, Oreoscoptes is doubtfully separable from it.
- GK 9. Dumetella carolinensis. We follow Monroe (1968) in considering the Catbird monotypic. D. c. ruficrissa (Aldrich, 1946) may be recognizable, but this is doubtful (see Rand and Traylor, 1949). However, D. c. meridianus (Burleigh, 1959) is clearly not recognizable. We concur with Paynter's (1955) merger of Melanoptila (1858) into Dumetella (1837), and feel indeed that glabrirostris is very closely related to carolinensis.

- GL 1. Turdus migratorius. We follow Ripley (1964) and others in considering the Baja California endemic confinis conspecific with migratorius. Variation in some subspecies was discussed by Todd (1963) and by Mengel (1965). The many species in the genus, effects of little-studied sympatric interactions and possible convergence in New World and Old World lines, and our general lack of knowledge of the morphology and habits of most species militate against an attempt to group the species at this time. Among New World species, rufopalliatus and rufitorques are especially similar to migratorius in juvenal and adult plumages, but various Old World species (obscurus, dissimilis, etc) also may be closely related.
- GL 2. Zoothera naevia. Racial separation within this thrush is questionable; only females can be assigned to subspecies. We accept Ripley's (1952) assignment of this species to Zoothera (rather than comprising the monotypic Ixoreus). None of its Old World relatives are very closely related, but those nearest naevia may include citrina, gurneyi, and siberica (all Asian). Zoothera (Ridgwayia) pinicola of Mexico may be closely related to naevia; Short is impressed by their similarity in the field and Phillips (in Phillips, et al., 1964) has remarked on their resemblances.
- GL 3. Hylocichla mustelina. This monotypic species has been generically separated from the next four species on valid grounds by Dilger (1956a, 1956b). It has been noted that the Wood Thrush resembles species of *Turdus* in habits, but we suggest that it might be closer to *Zoothera* (spp.).
- GL 4. Catharus guttatus. Dilger (1956a, 1956b) has demonstrated that this species forms a species group with ustulatus, minimus, and fuscescens, and that these four species belong to the genus Catharus, rather than to Hylocichla. Variation in the Hermit Thrush has been reviewed by Phillips (1961; also in Phillips, et al., 1964) and recently by Aldrich (1968).
- GL 5. Catharus ustulatus. Variation in this thrush has been discussed by Todd (1963), by Phillips (in Phillips, et al., 1964), and by Bond (1963). (See GL 4.)
- GL 6. Catharus minimus. This species may be nearest fuscescens (Todd, 1963). (See GL 4.)
- GL 7. Catharus fuscescens. Variation in the Veery was discussed by Burleigh and Duvall (1959). Todd (1963) has suggested that it is closely related to minimus. (See also GL 4.)
- GL 8. Sialia sialis. Phillips (in Phillips, et al., 1964) briefly compared northern races of this bluebird while Dickey and van Rossem (1930) considered some southern forms. The genus Sialia comprises a closely knit group sharply separated from Old World relatives.
  - GL 9. Sialia mexicana. Phillips (in Phillips et al., 1964) has com-

- mented on the races of the Western Bluebird. The species probably represents an early offshoot of bluebirds in the New World, evolving as the western counterpart of *sialis* in a situation comparable to that of the blue jays (*Cyanocitta cristata* and *stelleri*). Thus *sialis* and *mexicana* constitute an ancient species pair.
- GL 10. Sialia currucoides. The Mountain Bluebird is closely related to the other bluebirds and has hybridized with sialis (Lane, 1968).
- GL 11. Oenanthe oenanthe. Eurasian forms of this wheatear were reviewed by Vaurie (1949). Several races are well differentiated, especially phillipsi (Somaliland) and seebohmi (North Africa), which have been considered specifically distinct by various earlier authors.
- GL 12. Luscinia svecica. Variation in svecica has been discussed by Vaurie (1949, 1959). The svecica and cyanecula groups are well differentiated and interbreed in a secondary contact. The Bluethroat has no very close relatives.
- GL 13. Myadestes townsendi. The race calophonus described by Moore (1937) is weakly defined. Relationships within the genus are uncertain but obscurus (northern Middle America) and elisabeth (Cuba), and possibly unicolor (Middle America), may be related to townsendi.
- GM 1. *Phylloscopus borealis*. Races of this principally Palearctic species were considered by Vaurie (1959). For a monograph of this genus see Ticehurst (1938).
- GM 2. Regulus [regulus]. Van Rossem (1945a) briefly discussed some races of R. satrapa, which has been merged, or its relationship suggested by various authors with regulus on the one hand and ignicapillus on the other hand. We consider it related to regulus (see Mayr, 1956), with which it forms a superspecies. Further studies are needed, particularly of the relationships of goodfellowi (Formosa). R. satrapa has hybridized with R. calendula (Gray, 1958).
- GM 3. Regulus calendula. Variation in this kinglet has been discussed by Phillips (1964; see also Phillips, in Phillips, et al., 1964). It appears not to be related closely to other kinglets, although it has hybridized with R. satrapa (Gray, 1958). (See GM 2.)
- GM 4. Polioptila caerulea. Races of this gnatcatcher were discussed by Grinnell (1926) and by van Rossem and Hachisuka (1937). The species is undoubtedly closely related to melanura, but studies of other species in the genus are necessary to elucidate their precise relationships.
- GM 4. Polioptila melanura. Grinnell (1926) discussed races of this gnatcatcher. (See GM 4.)
- GN 1. Motacilla flava. There is great divergence of opinion among recent students about the taxonomy of this wagtail (see Vaurie 1957a, 1959; Sammalisto, 1961, and references therein). Some of the morphologically most divergent forms (e.g., the flava, thunbergi, feldegg, etc. groups) meet in areas of secondary contact, but it is controversial how

extensive the interbreeding is in areas of overlap. Several of these forms are sometimes treated as distinct species.

- GN 2. Anthus spinoletta. Old World races of this pipit have been discussed by Vaurie (1959) and some North American races are treated by Phillips (in Phillips, et al., 1964). There are two morphologically and ecologically divergent racial groups (spinoletta and petrosus groups; Vaurie, 1959), which have been considered specifically distinct. A. spinoletta appears to represent a recent invasion of the New World by pipits, A. spragueii perhaps representing an earlier invasion (see GN 3).
- GN 3. Anthus [furcatus]. We agree with Hall (1961), that A. spragueii is very similar to (and presumably closely related to) South American A. furcatus. However, merging the two species would seem premature in view of our lack of knowledge of the other South American pipits. Hence, we consider them to comprise a superspecies, probably related to the Old World A. campestris complex (Hall, 1961). If furcatus is not related to other South American species, then the latter have no North American relative and their relationship with Old World species thus would remain to be established.
- GO 1. Bombycilla garrulus. Races of garrulus have been discussed by Vaurie (1958) and characterized by Arvey (1951). The three species of waxwings are very closely related (Arvey, 1951).
- GO 2. Bombycilla cedrorum. Races of the Cedar Waxwing described by Burleigh (1963) are not sufficiently marked to be recognized; the species is monotypic (Short, unpubl.; see also Monroe, 1968).
- GP 1. Phainopepla nitens. Races of the Phainopepla, which lacks close relatives, were diagnosed by Arvey (1951).
- GQ 1. Lanius [excubitor]. Variation in L. excubitor was discussed by Vaurie (1955b, 1959), while Miller (1931) is the standard work on forms of L. ludovicianus (however, see Phillips' comments in Phillips, et al., 1964), as well as on the North American races of excubitor. L. ludovicianus is a small, generally dark, southern shrike which is allopatric with paler, larger, northern excubitor. This exactly parallels the Palearcitic situation; a generally smaller and darker southern form (meridionalis group) is allopatric with a northern paler and larger form (excubitor group). The two Palearctic groups are generally accepted as being conspecific, and ludovicianus may likewise prove to be conspecific with them. We tentatively treat excubitor, ludovicianus, and East Asian sphenocercus as component species of a superspecies. It remains to be determined whether sphenocercus and excubitor are in contact in China or Mongolia (Vaurie, pers. comm.). Relationships within Lanius are unclear, but at least these appear to comprise a species group; [excubitor], dorsalis (Africa), excubitorides (Africa), somalicus (Africa), schach (southeastern Asia, East Indies to New Guinea), tephronotus (central Asia), and minor (western Eurasia).

- HA 1. Vireo huttoni. Relationships indicated among the vireos largely follow Hamilton (1958, 1962). Some racial information for polytypic species of vireos is contained in Hamilton (1958). This species appears related to atricapilla and perhaps to solitarius and its relatives.
- HA 3. Vireo [griseus]. Burleigh and Lowery (1945) reviewed races of V. griseus. The strongly differentiated West Indian white-eyed vireos (crassirostris, modestus, caribaeus, and gundlachii) are considered by us conspecific with griseus; each is sometimes considered a distinct species (Bond, 1968, considered caribaeus possibly conspecific with pallens, rather than with griseus). Middle American pallens is a close relative of griseus and comprises a superspecies with it. This superspecies forms a species group with bellii, vicinior, latimeri (Puerto Rico), carmioli (mountains of southern Middle America), bairdi (Cozumel Island), and nelsoni (western Mexico). V. carmioli is only questionably a member of the group (see Eisenmann, 1962b.)
- HA 6. Vireo solitarius. Races of this vireo were reported upon by Hamilton (1958). The eastern solitarius group is allopatric with the western plumbeus group of races, with a gap in British Columbia and southern Alberta. The Yellow-throated Vireo (flavifrons) is closely related to solitarius, and they have hybridized (see Blake, 1968); they may comprise a superspecies.
- HA. 8. Vireo philadelphicus. This monotypic vireo is one component of the species group including hypochryseus (western Mexico), the superspecies olivaceus, and gilvus.
- HA 9. Vireo [olivaceus]. Following various authors (see, e.g., Meyer de Schauensee, 1966) we consider the Central American flavoviridis group, the South American chivi group, and gracilirostris (Fernando de Noronha Island) as conspecific with olivaceus. The habits, vocalizations, and morphology of these forms are very similar (Short, pers. obser. of olivaceus, chivi, and flavoviridis groups). Vireo altiloquus, essentially the West Indian representative of olivaceus, comprises a superspecies with the latter. We consider the North American populations of olivaceus a single subspecies (see also Monroe, 1968). (See also HA 8.)
- HA 10. Vireo gilvus. We follow various authors in merging Middle and South American leucophrys into gilvus, although these may prove specifically distinct (Monroe, 1968). Phillips (in Phillips, et al., 1964) discussed various races of gilvus. (See also HA 8.)
- HB 1. Mniotilta varia. This endemic, monotypic species is of uncertain relationships, but its relatives will probably be found among the dendroicas.
- HB 2. Vermivora bachmanii. Vermivora probably represents a polyphyletic assemblage with subgroups related independently to Dendroica. V. bachmanii seems closely related to V. pinus and V. chrysoptera, and these are closely related to Dendroica (penyslvanica?).

- HB 3. Vermivora [pinus]. Vermivora pinus and V. chrysoptera exhibit essentially allopatric distributions, but they overlap broadly and hybridize extensively (Short, 1963; 1969b; see also Ficken and Ficken, 1968). Considerable hybridization merits their designation as component species of a superspecies, despite their widespread overlap. V. pinus has hybridized also with Oporornis formosus (Gray, 1958). (See HB 2.)
- HB 4. Vermivora peregrina. This warbler is probably a distant relative of the celata-ruficapilla group.
- HB 5. Vermivora celata. The Orange-crowned Warbler probably is rather closely related to the ruficapilla complex, contra Mengel (1964). Phillips (in Phillips, et al., 1964) provided a good summary of its races.
- HB 6. Vermivora [ruficapilla]. The three warblers (ruficapilla, virginiae, and crissalis) of this complex are closely related, allopatric forms, tentatively considered as component species of a superspecies (Mengel, 1964), although they are conceivably conspecific (Phillips, in Phillips, et al., 1964). Field studies are needed in southeastern Idaho and northern Utah where virginiae and ruficapilla may meet. These species comprise a species group with luciae and celata.
- HB 7. Vermivora luciae. Superficially quite similar to the ruficapilla complex, it comprises a species group with the latter and V. celata, but its distinctive habits, vocalizations, and ecology suggest that its relationship to ruficapilla is about as distant as that of celata.
- HB 8. Parula americana. Chapman (1925) reviewed various forms here considered conspecific with americana, following Paynter (1957b) and Phillips (1962). The americana, pitiayumi, and graysoni (Socorro Island) racial groups formerly have been considered specifically distinct. The Parula Warbler has hybridized with Setophaga ruticilla and with Dendroica dominica (Gray, 1958; see also HB 13).
- HB 9. Dendroica petechia. Included within petechia are the various tropical Yellow Warblers (petechia of the West Indies, various islands, and northern South America; erithachorides of Middle and northern South American mangrove areas) and the North American aestiva group (see Aldrich, 1942; Phillips, in Phillips, et al., 1964; and Monroe, 1968). Races of the aestiva group were discussed by Phillips.
- HB 12. Dendroica caerulescens. Races of this species are weakly developed (Monroe, 1968) and it is best considered monotypic. Its relationships are uncertain but may be with D. caerula.
- HB 13. Dendroica [dominica]. Disjunct dominica, graciae, adelaidae (Puerto Rico region), and pityophila (Cuba) appear closely related and comprise a superspecies (Mengel, 1964). Webster (1961) discussed variation in D. graciae. D. dominica and pityophila are sympatric in the Bahama Islands. D. dominica has hybridized with Parula americana (Haller, 1940); the two hybrids, adult birds collected 18 miles apart in West Virginia, were described as D. potomac.

- HB 14. Dendroica nigrescens. We consider this species to be monotypic (but see Phillips, in Phillips, et al., 1964). (See HB 15.)
- HB 15. Dendroica [virens]. Evolution of this group of warblers, including D. nigrescens, was discussed by Mengel (1964). D. virens, occidentalis, and townsendi are considered species comprising a superspecies. D. occidentalis and D. townsendi meet and slightly overlap in western Washington; they hybridize infrequently (Jewett, 1944). We treat chrysoparia as a race of virens (see Short, quoted by Mengel, 1964), and feel D. v. "waynei" is not sufficiently distinct to warrant recognition (see Monroe, 1968). D. nigrescens is a close relative of this complex and fusca may be somewhat more distantly related.
  - HB 16. Dendroica fusca. (See HB 15.)
- HB 17. Dendroica pinus. Racial features were noted in Griscom, et al. (1957). (See HB 18.)
- HB 18. Dendroica [discolor]. D. discolor and D. vitellina (Cayman and Swan Islands) are very closely related (Bond, 1961) and are treated here as comprising a superspecies. These species appear to be relatives of D. pinus and possibly of D. palmarum.
- HB 19. Dendroica palmarum. Races of the Palm Warbler are characterized in Griscom, et al. (1957). (See HB 18.)
- HB 20. Dendroica tigrina. Relationships of this warbler are probably with D. coronata and D. magnolia (Mengel, 1964).
  - HB 21. Dendroica magnolia. (See HB 20.)
- HB 22. Dendroica coronata. The coronata and auduboni subspecies groups hybridize in the Northwest; recent studies of Hubbard (1969) indicate that they are conspecific (see also Phillips, in Phillips, et al., 1964, who also discussed various races). The auduboni group comprises several races, but the eastern coronata group is monotypic (Monroe, 1968). (See HB 20.)
- HB 23. Dendroica kirtlandii. Mengel (1964) suggested that this warbler is a relict species related to the dominica group, but we are not certain of this.
- HB 24-25. Dendroica striata and D. castanea. The Blackpoll seems closely related to D. castanea; they have hybridized (Brodkorb, 1934). D. striata has also hybridized with Seiurus noveboracensis (Short and Robbins, 1967).
- HB 26. Setophaga ruticilla. The genus Setophaga (1827) is probably best merged in Dendroica (Parkes, 1961; Ficken and Ficken, 1965); we maintain it pending studies of various warblers, including species of Dendroica and Vermivora, to establish more precisely its affinities. It has hybridized with Parula americana (Gray, 1958). We consider the Redstart to be monotypic (see Monroe, 1968, and also Wetmore, 1949).
  - HB 27. Seiurus aurocapillus. The races of Ovenbird are weakly

- defined (Miller, 1942). This genus is closely allied with *Dendroica* (Short and Robbins, 1967).
- HB 28. Seiurus noveboracensis. The Northern Waterthrush is more closely related to S. motacilla than to S. aurocapillus. Conceivably it could be considered to comprise a superspecies with motacilla; the two overlap only narrowly and are ecologically separated. It exhibits "mosaic" variation and recognition of substantive races is impossible (Eaton, 1957). It has hybridized with Dendroica striata (Short and Robbins, 1967).
- HB 30-31. Helmitheros swainsonii and H. vermivorus. Limnothlypis (1914) is merged into Helmitheros (1819) following Griscom (in Griscom, et al., 1957). Both species are considered monotypic.
- HB 32. Protonotaria citrea. This is another species of uncertain relationships, although having affinities with Dendroica. Beardslee and Mitchell (1965) report instances of a Prothonotary Warbler singing the song of Dendroica petechia and of the former tending nests and feeding young of the latter. The behavior at the nest may not be significant, however, considering how often "helpers at the nest" are not closely related to the nest owners.
- HB 33. Geothlypis trichas. Variation in this yellowthroat was discussed by Behle (1950; see also Phillips, in Phillips, et al., 1964, and Griscom, et al., 1957). G. flavovelata (eastern Mexico) was merged in "beldingi" (Baja California), and chapalensis (Jalisco, Mexico) into trichas by Miller, et al. (1957). We consider all of these conspecific. G. nelsoni (southeastern Mexico) is closely related to trichas.
- HB 34. Geothlypis poliocephala. Like Eisenmann (1962a) and others, we merge Chamaethlypis (1887) into Geothlypis (1847). Wetmore (1944) reviewed races of poliocephala. Its closest relative is the South American G. aequinoctialis, which quite possibly forms a superspecies with it (Short, pers. obser.).
- HB 35. Oporornis formosus. This species is not very closely related to others of the genus. It has hybridized with Vermivora pinus (Gray, 1958). Oporornis is related to Geothlypis, but not considered by us congeneric, contra Lowery and Monroe (1968).
  - HB 36. Oporornis agilis. (See HB 37.)
- HB 37. Oporornis philadelphia. Closely similar, essentially allopatric philadelphia and tolmiei hybridize in Alberta (recent studies of G. Cox, unpubl.) and are considered conspecific by us. They are usually treated as separate species. Races of O. "tolmiei" were treated by Phillips (1947), but they are so weakly characterized that we do not recognize them (see also Monroe, 1968). O. agilis is closely related to philadelphia.
- HB 39. Wilsonia pusilla. Phillips (in Phillips, et al., 1964) discussed variation in this warbler. The species of this genus are quite distinct inter se, and their relationships with other genera are unclear.

- HB 41. Myioborus pictus. We follow Parkes (1961) and Ficken and Ficken (1965) in merging this species in Myioborus, rather than maintaining it in Setophaga.
- HB 42. Peucedramus taeniatus. This species has been removed from the Parulidae by George (1962), who considered its relationships uncertain but probably with certain Old World oscines. However, Webster (1962), using other anatomical characters disagreed and concluded that the Olive Warbler is a true wood warbler. Recent studies (Bock, pers. comm.) of the hyoid and jaw musculature suggest that it is a nine-primaried oscine and perhaps belongs within or close to the Parulidae. Webster (1958) discussed its variation.
- HB 43. Icteria virens. The Yellow-breasted Chat is of uncertain affinities (see Eisenmann, 1962a); it may not be a wood warbler. Its variation is simple with weakly defined eastern and western races.
- HC 1. Dolichonyx oryzivorus. This species is a bunting-like icterid probably related to Sturnella (sensu lato) and Agelaius (Short, pers. obser.; see also Short, 1968b). For this reason we do not follow Blake's (1968) placement of Dolichonyx in a subfamily apart from other blackbirds. Furthermore, the following sequence of icterids does not follow Blake's arrangement because Dolichonyx, Agelaius, and Sturnella appear relatively less specialized than the orioles and oropendolas which commence Blake's list, but should be last as highly specialized derivatives (Short and Bock, 1970).
- HC 2. Sturnella [magna]. S. magna and S. neglecta form an emergent superspecies; they are essentially allopatric but hybridize infrequently in an area of overlap and this area of sympatry appears to be increasing (Lanyon, 1957, 1966; Szijj, 1966; Short, 1968b). They are also considered sibling species. Populations assigned to magna include northern South American meridionalis, paralios, and praticola, which generally sing magna-like songs but somewhat resemble neglecta in their morphology. These forms are in need of further study. Saunders' (1932) review of magna is the most recent that is available. Races of neglecta are poorly defined (Phillips, in Phillips, et al., 1964), and and we consider this species monotypic, as does Blake (1968). These meadowlarks are related to the South American "Pezites" group, especially Sturnella bellicosa and S. loyca (formerly races of "Pezites" militaris; see Short, 1968b).
- HC 3. Agelaius phoeniceus. The Redwinged Blackbird is in need of a continent-wide study of its variation (for variation see Howell and van Rossem, 1928; Phillips in Phillips, et al., 1964; Mengel, 1965; and Dickerman, 1965). Interbreeding of distinctive races occurs in Mexico (Dickerman, 1965; Hardy and Dickerman, 1965; Hardy, 1967); these races include gubernator and nelsoni. Cuban races (subniger, assimilis) are also well differentiated and have been considered specifically distinct. (See HC 4.)

- HC 4. Agelaius tricolor. The Tricolored Blackbird is closely related to A. phoeniceus and probably to West Indian A. humeralis and A. xanthomus.
- HC 5. Xanthocephalus xanthocephalus. This blackbird is of uncertain relationships, but it is probably related to Agelaius.
- HC 6. Quiscalus [mexicanus]. Selander and Giller (1961) have shown that major and mexicanus breed sympatrically without hybridization in eastern Texas and western Louisiana. These sibling species comprise a superspecies. Selander and Giller's interpretation has been criticized by Phillips (in Phillips, et al., 1964), who discussed variation in western forms of mexicanus and interbreeding in secondary contacts between the moderately differentiated races nelsoni and monsoni. The well-marked Mexican highland Q. m. palustris is often considered specifically distinct. We follow Blake (1968) in merging Cassidix (1831) into Quiscalus (1816).
- HC 7. Quiscalus quiscula. A broad to narrow zone of hybridization between the quiscula and versicolor groups characterizes variation in this grackle. This hybridization has been studied most recently by Huntington (1952) and by Yang and Selander (1968). Racial characters are given by these authors. Allopatric West Indian niger and lugubris, and nicaraguensis of Nicaragua appear closely related to quiscula (Yang and Selander, 1968), perhaps forming a superspecies with the latter.
- HC 8-9. Euphagus carolinus and E. cyanocephalus. These closely related species exhibit an essentially allopatric distribution. Perhaps they constitute a superspecies but their considerably different habits and ecology indicate that they are sufficiently distinct to place them instead within a species group. We do not recognize E. carolinus nigrans (Burleigh and Peters, 1948). Relationships of Euphagus with other genera are uncertain.
- HC 10. Molothrus aeneus. Variation in this cowbird was discussed by van Rossem (1934) and by Parkes and Blake (1965). We follow the latter authors in merging Tangavius (1839) in Molothrus (1832). However aeneus shows affinities with Scaphidura; it should not be placed between ater and the other species of Molothrus related more closely to ater, but should follow the latter (thus preceding Scaphidura).
- HC 11. Molothrus ater. Western races of Brown-headed Cowbirds were discussed by Phillips (in Phillips, et al., 1964). Friedmann (1929) considered relationships within Molothrus (including "Tangavius"), but it is uncertain which of the South American species is the closest relative of ater.
- HC 12. Icterus gularis. This oriole may be related to I. nigrogularis of northern South America as suggested by Beecher (1950), despite their widely separate positions in Blake's (1968) list.
- HC 13. Icterus cucullatus. Phillips (in Phillips, et al., 1964) discussed variation in this oriole. Its relationships are not clear but may be with dominicensis (West Indies, Middle America) or with graduacauda.

- HC 14. Icterus galbula. The species is comprised of three morphologically distinct groups of populations, the galbula group, the bullockii group, and the abeillei group (Mexico). These interbreed to form hybrid zones in the Great Plains (galbula, bullockii; see Sibley and Short, 1964) and in Durango, Mexico (bullockii, abeillei; Short, unpubl.). All are considered conspecific. Following Beecher (1950), Middle American pustulatus is considered a close relative of galbula, and comprises a species group with the latter. Females of pustulatus are virtually identical to subadult males of the bullockii group of I. galbula, while females of the galbula group of the latter species have the spotted back of pustulatus. I. sclateri is also a close relative of these species.
- HC 15. Icterus spurius. Variation in the Orchard Oriole was considered by Dickerman and Warner (1962). Mexican fuertesi is a well-marked subspecies. The relationships of spurius are uncertain but they may lie with galbula (contra Beecher, 1950). Although broadly sympatric with galbula, the ranges of spurius and galbula seem to be mutually exclusive in some areas (e.g., the Maryland "fall line" region; Short, pers. obser.), suggesting that they interact.
- HC 16. Icterus graduacauda. Races of this oriole were discussed by van Rossem (1938). I. graduacauda is probably not related to I. icterus, as suggested by Beecher (1950).
- HC 17. Icterus parisorum. This is one of the thin-billed orioles considered by Beecher (1950) as comprising a genus ("Bananivorus") apart from Icterus. Its plumage pattern much resembles that of I. galbula, but its relationships remain to be established. Plumage patterns of about all of the North American orioles, particularly females (I. cucullatus, spurius, parisorum, and galbula), show remarkable similarities, which may reflect their close relationship, or parallelism (Hamilton, 1961), or both.
- HD 1. Piranga [olivacea]. The tanagers P. olivacea and P. ludoviciana are completely allopatric and closely related. They have hybridized (Tordoff, 1950; Mengel, 1963), and are considered to comprise a superspecies. The hybrids apparently resulted from wandering individuals of ludoviciana entering the range of olivacea and mating with individuals of the latter, for ludoviciana has been known to breed in Wisconsin (A.O.U., Check-list, 1957). Although they differ in ecology, their habits and certain vocalizations are quite similar (Short, unpubl.). P. leucoptera of Middle and South America is a close relative of these species.
- HD 2. Piranga flava. Variation in some forms of flava was considered by Howell (1965). The well-differentiated hepatica, lutea (South America), and flava (South America) groups are possibly specifically distinct, especially the latter (Meyer de Schauensee, 1966). (See HD 3.)
- HD 3. Piranga rubra. Variation in rubra was discussed by Phillips (in Phillips, et al., 1964). This tanager is rather closely related to P. flava and probably represents an offshoot of it. Its range overlaps that of flava

- in Arizona, New Mexico, and northwestern Mexico, but the two are ecologically separated. In the overlap region *rubra* occurs in lowland riparian (willow-cottonwood) woods, while *flava* is an upland pine-oak woodland bird. However, *rubra* prefers both pine and oak woods in the East where *flava* is absent. The varied ecology of diverse subspecies groups within *P. flava* (see HD 2) suggests that *rubra* could well comprise a superspecies with *flava*.
- HE 1. Carpodacus [erythrinus]. This species commences the subfamily Carduelinae. C. purpureus is very closely related to C. erythrinus of Eurasia and is considered to comprise a superspecies with it. Duvall (1945b) and Rand (1946) discussed variation in purpureus. (See HE 2 and HE 4.)
- HE 2. Carpodacus cassinii. Cassin's Finch is closely related to C. purpureus and can be considered a sibling species with it (possibly cassinii is part of the superspecies [erythrinus]). There is slight variation (Duvall, 1945b) in this finch but we consider it monotypic.
- HE 3. Carpodacus mexicanus. The House Finch exhibits extreme individual and geographic variation. Insular (west coastal Baja California) amplus and megregori are believed conspecific with mexicanus; they are often considered specifically distinct. Various races were discussed by Moore (1939a, 1939b). Conceivably mexicanus and cassinii represent an older invasion of Carpodacus from Eurasia, and purpureus a more recent entrant into North America.
- HE 4. Pinicola enucleator. Variation in the Pine Grosbeak has been discussed by Vaurie (1956b) and by Todd (1963). Its relationships remain to be determined, but are obviously with Carpodacus; it has hybridized with C. purpureus (Gray, 1958; specimen seen by Short).
- HE 5. Loxia curvirostra. This very variable Holarctic species has been discussed by Griscom (1937), by Vaurie (1956b), and by Phillips (in Phillips, et al., 1964). Various more or less geographically isolated races are distinctive (scoticus, guillemardi of Cyprus, altaiensis and its relatives of Central Asia, himalayensis, etc.). Loxia pityopsittacus of Europe is closely related to curvirostra.
- HE 6. Loxia leucoptera. Hellmayr (1938) discussed variation in this species. An isolated race (megaplaga) occurs on Hispaniola.
- HE 7. Carduelis [spinus]. We consider Spinus (1816) congeneric with Carduelis (1760). The New World species comprise a subgroup of this genus, except for C. pinus which is closely related to Palearctic spinus (Vaurie, 1959); these species comprise a superspecies. There is a possibility that pinus is also related to certain New Word species such as barbatus (South America; see Todd, 1926), but is is more likely that Central and South American "siskins" are related instead to the following species of "goldfinches." Variation in pinus was discussed by Aldrich (1946) and by Todd (1963).

- HE 8. Carduelis tristis. The species has no close relatives; its variation is slight.
- HE 9. Carduelis psaltria. Populations of this species fall into two groups (psaltria and hesperophila) which freely interbreed (R. G. Wolk, pers. comm.). Its variation was discussed by Phillips (in Phillips, et al., 1964). Todd (1926) was probably correct in suggesting Middle and South American xanthogaster as a related species; these may comprise a species group.
- HE 10. Carduelis lawrencei. Lawrence's Goldfinch is probably related to one or another of the Central and South American species of Carduelis, rather than to tristis or psaltria.
- HE 11. Acanthis [flammea]. We follow Vaurie (1956a) and other authors in considering hornemanni specifically distinct from flammea; Salomonsen (1950) and Williamson (1961) regarded them as conspecific. We treat them as component species of a superspecies, for, although showing considerable (apparent) sympatry, they hybridize rather freely in some areas (Salomonsen, 1950; Brooks, 1968). They are also sibling species. Todd (1963) considered the rather well-marked race A. h. exilipes specifically distinct from hornemanni.
- HE 12. Leucosticte [arctoa]. We consider the New World forms (tephrocotis, atrata, australis) as well-marked races of polytypic, Holarctic arctoa. The variability found in rosy finches (Miller, 1939; Vaurie, 1956b) suggests that we should allow some latitude in variation among geographically isolated populations. French (1959) advocated merger of atrata with tephrocotis on the basis of its interbreeding with the latter. Mayr (1927) reviewed all of the forms of arctoa, stressing their relationship and suggesting their conspecificity. Asian L. brandti is a closely related largely allopatric species, considered to comprise a superspecies with arctoa. The two species are sympatric in the Altai Mountains (Vaurie, 1956b, 1959).
- HE 13. Coccothraustes vespertinus. Variation in this finch is discussed in Phillips (1962). It is sympatric with its close relative C. abeillei in Mexico. Paynter (1968) has merged Hesperiphona (1850), along with the Asian Eophona (1851) and Mycerobas (1847), into Coccothraustes (1760). We agree, except that Short concurs with Vaurie (pers. comm.) that Mycerobas should be excluded. It is "Eophona," which reaches Siberia, that contains species most closely related to the New World "hawfinches."
- HE 14. Spiza americana. We consider Spiza to be a primitive fringillid resembling somewhat the ancestral stock that gave rise to the Emberizinae and Cardinalinae. Since early icterids were probably finchlike, it is not surprising that Spiza shows some similarities with the Icteridae (Beecher, 1950). This species commences the Cardinalinae.
  - HE 15. Cardinalis [cardinalis]. The Cardinal is badly in need of

an over-all revision. Its relationships are with South American phoeniceus, the two species comprising a superspecies. C. phoeniceus is large-billed, thus approaching C. sinuata, but its general resemblance to cardinalis and the latter's variability and greater proximity to the range of phoeniceus indicate that cardinalis may be more closely related to phoeniceus than to sinuata. The name Cardinalis (see Opinion 784, Bull. Zool. Nomencl., 23: 201-203, 1966) is no. 1728 on the Official List of Generic Names.

- HE 16. Cardinalis sinuata. Pyrrhuloxia (1850) is merged in Cardinalis (1838) following Bock (1964; see also Gould, 1961). The latest revision is that of van Rossem (1934).
- HE 17. Pheucticus [ludovicianus]. The grosbeaks P. ludovicianus and P. melanocephalus hybridize in a zone of overlap in the Great Plains; interbreeding is apparently not random (West, 1962; Short, 1969a). West considered them conspecific. Because their interbreeding is limited, presumably owing to the existence of isolating mechanisms; we treat them as species comprising a superspecies (Short, 1969a). Races of melanocephalus are weakly defined (Phillips, in Phillips, et al., 1964). Relationships with Central and South American species of Pheucticus remain to be clarified.
- HE 18. Passerina caerulea. Races of this species were reviewed by Storer and Zimmerman (1959). We concur with Phillips (in Phillips, et al., 1964) that Guiraca (1827) is congeneric with Passerina (1816). Cyanocompsa and Cyanoloxia are closely related to Passerina, and these possibly are congeneric; however, we believe that they are related to Passerina independently of P. caerulea, and not through that species.
- HE 19. Passerina [cyanea]. The buntings P. cyanea and P. amoena hybridize in a zone of overlap in the Great Plains, but interbreeding is not random (Sibley and Short, 1959; Short, 1969a). This situation is similar to that of the grosbeaks (see HE 17), except that the overlap is greater and apparently is being extended. We consider these forms as species comprising a superspecies. Some authors (e.g., Phillips, in Phillips, et al., 1964) consider them conspecific, but the nature of their hybridization militates against this interpretation (Short, 1969a). (See also HE 20.)
- HE 20. Passerina versicolor. Races of the Varied Bunting are not strongly marked. With P. [cyanea] and P. ciris this species forms a species group; it has hybridized with P. ciris (Storer, 1961). The latter species overlaps broadly with versicolor.
- HE 21. Passerina ciris. Storer (1951) discussed variation in *P. ciris*. It has hybridized with *P. versicolor*, its probable closest relative; the two overlap over a considerable part of the range of *ciris*. (See HE 20.)
- HE 22. Sporophila torqueola. This variable species includes a number of well-marked races (torqueola, morelleti, sharpei) in northern Middle America. Some of the racial differences may actually be caused

by polymorphism (Monroe, 1968). Relatives include *S. americana*, *S. aurita*, and *S. collaris* (Meyer de Schauensee, 1952). This species introduces the Emberizinae.

HE 23. Arremonops [rufivirgata]. Northern South American A. tocuyensis is closely related and possibly conspecific witth rufivirgata (Hellmayr, 1938); the two comprise a superspecies. The rufivirgata group and the disjunct (Costa Rica) superciliosa group are well-differentiated and have been considered specifically distinct. Monroe (1963) discussed some relationships within the genus, while Sutton and Burleigh (1941) treated variation in rufivirgata.

HE 24. Pipilo chlorurus. We merge Chlorura (1862) into Pipilo (1816) following Sibley (1955). This species may be related to P. ocai.

HE 25. Pipilo erythrophthalmus. There are several distinctive groups of races of erythrophthalmus, most of which have been considered specifically distinct at one time or another. The southeastern alleni group of races hybridizes with the erythrophthalmus group where they meet (Dickinson, 1952). The western maculatus group hybridizes with the eastern erythrophthalmus group in the Great Plains (Sibley and West, 1959). The Mexican ocai group hybridizes with the maculatus group in southern Mexico (Sibley, 1950; see references in Sibley and Sibley, 1964); the two groups are sympatric without apparent interbreeding in three small areas. Effects of their interbreeding are widespread and the hybrid zones are extensive, and hence Short considers them conspecific (Short, 1969a). Mayr rather would emphasize their sympatry and the distribution of erythrophthalmus beyond ocai to the south by considering ocai a species, an element of the superspecies erythrophthalmus. The Socorro Island subspecies socorroensis is also distinctive, but the extensive hybridization between the more divergent ocai and maculatus groups suggests that socorroensis is conspecific with erythrophthalmus. Various races were treated by Dickinson (1952) and by Sibley (1950). P. chlorurus appears to be closely related to ocai (erythrophthalmus).

HE 26. Pipilo [fuscus]. The Brown and Abert towhees are closely related (Marshall, 1960, 1964b) and comprise a superspecies with P. albicollis of southern Mexico (Davis, 1951). Although the ranges of aberti and fuscus would seem to indicate extensive sympatry, Phillips (in Phillips, et al., 1964) has noted that the two species are in contact or overlap in only three small areas. Likewise, albicollis and fuscus meet barely, if at all, in southern Mexico (Davis, 1951). No hybrids have been reported among these groups. Phillips (1963) discussed racial variation in aberti while racial variation and relationships in fuscus were considered in Grinnell and Swarth (1926), in Moore (1949), and in Marshall (1960); Davis (1951) discussed variation in both species. The eastern (mesoleucus or perpallidus) group and western (crissalis) group of P. fuscus are morphologically divergent and allopatric (Davis, 1951).

- HE 27. Calamospiza melanocorys. Relationships of this monotypic bunting are uncertain, but they may be with the longspurs (Calcarius).
- HE 28. Animodramus sandwichensis. We do not consider the Ipswich Sparrow (princeps) of Cape Sable Island specifically distinct (Beecher, 1955), as do many authors. Variation in sandwichensis has been discussed by Peters and Griscom (1938), Camras (1940), Aldrich (1940), van Rossem (1947c), and Dickerman and Parkes (1960). We follow Phillips (in Phillips, et al., 1964), Murray (1968), and others in merging Passerculus (1838) in Animodramus (1827). A hybrid A. sandwichensis X A. savannarum indicates, with other evidence (Dickerman, 1968), the rather close relationship of these species. Short (unpubl.) suspects that the South American grassland sparrows of the genus Myospiza (1898, actually a superspecies) also may be very closely related to savannarum.
- HE 29. Animodramus bairdii. This monotypic species is most closely related to A. savannarum.
- HE 30. Ammodramus savannarum. Variation in some North American populations was discussed by Phillips (in Phillips, et al., 1964). The North American (pratensis) group of migratory Grasshopper Sparrows is well differentiated from the West Indian-Middle American savannarum group. The Grasshopper Sparrow has hybridized with A. sandwichensis. Recent discussions (e.g., Murray, 1968; Dickerman, 1968) of relationships of this group leave something to be desired (see HE 28). Pending consideration of the relationships of Myospiza with Ammodramus, assignment of species to species groups is unwarranted.
- HE 31. Ammodramus henslowii. Brewster (1918) discussed variation in this grassland sparrow. Murray (1968) offered rather convincing evidence that Passerherbulus is diphyletic, henslowii being related to Ammodramus savannarum. We, therefore, follow his suggestion of placing henslowii in Ammodramus.
- HE 32. Ammospiza leconteii (= Passerherbulus caudacuta Latham, 1790). Murray (1968), discussing a hybrid of this species and Ammospiza caudacuta Gmelin, 1788, concluded from various lines of evidence that the closest relative of leconteii is A. caudacuta. We concur. Thus Passerherbulus (1907) is synonymized with Ammospiza (1905); Passerherbulus caudacuta Latham becomes Ammospiza leconteii (see Murray, 1968). However, we are not fully convinced that Ammospiza is generically separable from Ammodramus (1827).
- HE 33. Ammospiza caudacuta. Variation in the Sharp-tailed Sparrow has been discussed by Todd (1942) and by Montagna (1942). The inland, freshwater subspecies nelsoni is well differentiated and apparently allopatric. Woolfenden (1956) compared caudacuta with maritima, its presumed near relative. However, Murray (1968) has convincingly shown that A. caudacuta is very closely related to A. leconteii (the former Passer-

herbulus caudacuta), and he suggests that both of these are related to maritima. Beecher (1955) ignored leconteii in tracing the possible evolution of caudacuta and maritima from a common ancestor. The three species constitute a species group related to Ammodramus. A. caudacuta has hybridized with A. leconteii (Murray, 1968) and has copulated in the wild with maritima (Montagna, 1942).

- HE 34. Ammospiza maritima. The well-marked, allopatric Florida races nigrescens and mirabilis are conspecific with maritima, as Beecher (1955) suggested. They are often considered as separate species. Griscom (1944) has studied the species most recently. (See HE 33.)
- HE 35. Pooecetes gramineus. Variation in this species, of doubtful affinities, has been discussed most recently by Phillips (1964). The Vesper Sparrow has hybridized with Spizella pusilla (Doolittle, 1929).
- HE 36. Chondestes grammacus. Races of this distinctive species are weakly differentiated. Its relationships are uncertain, but may lie with Aimophila (belli?).
- HE 37. Aimophila carpalis. The variation of this sparrow has been discussed by Moore (1932, 1946); its races are weakly differentiated. It appears to have no close relatives (Storer, 1955), but it may link Spizella with Aimophila (Pitelka, 1951a).
- HE 38. Aimophila ruficeps. Variation in this sparrow was discussed by Burleigh and Lowery (1939) and by van Rossem (1947b). Its relationships within the genus are uncertain (Storer, 1955).
- HE 39. Aimophila aestivalis. Variation in aestivalis was discussed by Wetmore (1939). It is closely related to A. botterii and A. cassinii (Storer, 1955), and is allopatric with both. We tentatively maintain these as components of a species group, although aestivalis may comprise a superspecies with one of the other (cassinii?) two species.
- HE 40. Aimophila botterii. Races of botterii were reviewed by Phillips (1943), by Webster (1959), and by Howell (1965). Webster argued for the conspecificity of petenica (Middle America) and botterii; we follow him and Howell in treating them as conspecific. A. botterii is closely related to aestivalis and to cassinii (Storer, 1955), comprising a species group with them.
- HE 42. Aimophila bilineata. We follow Phillips (in Phillips, et al., 1964) in merging Amphispiza (1874) into Aimophila (1837). A. bilineata and A. belli are closely related, comprising a species group within Aimophila. Burleigh and Lowery (1939) and van Rossem (1945b) reviewed races of bilineata.
- HE 43. Aimophila belli. The western (belli) and eastern (nevadensis) groups are morphologically divergent and were long treated as separate species. (See HE 36 and HE 42.)
- HE 44. Spizella arborea. Races of arborea are weakly defined. Relationships within Spizella are not well established. This species appears

to have no very close relatives. Short feels that *Spizella* may be related to both *Aimophila* and *Junco* (sensu Short, see HE 50-57). (See also HE 37.) Some species of *Emberiza* are also similar.

HE 45. Spizella passerina. Some races of passerina were discussed by Phillips (in Phillips, et al., 1964). S. pallida and S. breweri are very closely related to passerina, and these species comprise a species group. S. passerina has hybridized with S. pallida (Storer, 1954).

HE 46. Spizella pallida. This monotypic sparrow is closely related to breweri; the two species apparently have hybridized (Gray, 1958), and they conveivably comprise a superspecies. They overlap in a narrow zone from southern Alberta to northwestern Nebraska. (See also HE 45.)

HE 47. Spizella breweri. Races of breweri were discussed by Swarth and Brooks (1925). (See also HE 45 and HE 46.)

HE 48. Spizella pusilla. Racial variation in the Field Sparrow was discussed by Wetmore (1939). S. wortheni of Mexico appears to be its closest relative, but relationships within Spizella are not sufficiently clear for us to establish that wortheni and pusilla form a superspecies. It is certainly premature to merge these species as Burleigh and Lowery (1942b) suggested. Rather, they comprise a species group related to the S. passerina complex. (See also HE 45.)

HE 49. Spizella atrogularis. Miller (1929) discussed variation in this sparrow, which may be related to the *S. passerina* complex, although its relationships are in need of study.

HE 50-57. The generic arrangement of the complex of North American species, traditionally assigned to the genera Junco (1831), Zonotrichia (1832), Passerella (1837), and Melospiza (1858), is still highly controversial. Melospiza was combined with Passerella by Linsdale (1928a, b), and Paynter (1964) merged both into Zonotrichia. Short (Short and Simon, 1965) would combine the enlarged genus Zonotrichia (sensu Paynter) with Junco chiefly owing to the frequency of interbreeding between Junco hyemalis and Z. albicollis. Mayr (pers. observ.) is impressed by the similarities of many of these species with species of Old World Emberiza. In view of the many contradictory suggestions it would seem advisable for the time being to adopt a conservative course, except for the generally accepted merging of Passerella and Melospiza. It will require new data (behavioral, anatomical, biochemical) to determine which species are most closely related to each other, and how they are related to Emberiza, Spizella, and Phrygilus (South America).

HE 50. Passerella lincolnii. Lincoln's Sparrow is only moderately variable (Miller and McCabe, 1935).

HE 51. Passerella georgiana. Races of the Swamp Sparrow were reviewed by Godfrey (1949). P. georgiana and P. lincolnii apparently comprise a species group.

- HE 52. Passerella iliaca. The Fox Sparrow is highly variable. Its variation has been treated by Linsdale (1928a, b), by Oberholser (1946), and by Behle and Selander (1951). Distinctive races include the insular unalaschensis and insularis, as well as various continental races. The Fox Sparrow seems closely related to P. melodia.
- HE 53. Passerella melodia. The Song Sparrow is highly polytypic with many distinctive races, especially in the Southwest, on the West Coast, in Alaska and the Aleutian Islands, and in Mexico. This variation was discussed in Wetmore (1936), in Marshall and Behle (1942), in Marshall (1948), in Dickerman (1963), and in Marshall (1964a).
- HE 54. Zonotrichia querula. Distinctive Harris' Sparrow is not very closely related to any other species in the genus; its relationships remain to be clarified.
- HE 55. Zonotrichia leucophrys. The White-crowned Sparrow includes variable populations comprising several well-marked races (gambelii, leucophrys, and nuttalli groups). This sparrow is closely related to the atricapilla group. It has hybridized with P. melodia (Dickerman, 1961), as well as with Z. atricapilla (Miller, 1940). Banks (1964) discussed variation in leucophrys.
- HE 56. Zonotrichia [atricapilla]. The Golden-crowned Sparrow (atricapilla) is essentially allopatric with the White-throated Sparrow (albicollis), with slight contact in British Columbia (Sibley, 1956). We consider these to comprise a superspecies. We recognize the close relationship of leucophrys to this complex by considering all three species to comprise a species group. Z. atricapilla has hybridized with Z. leucophrys (Miller, 1940). Z. albicollis hybridizes occasionally with broadly sympatric J. hyemalis (Short and Simon, 1965), suggesting to Short that the leucophrys-albicollis-atricapilla group is closely related to the superspecies hyemalis. Perhaps these two groups evolved from a common ancestor prior to the recent radiation within each group.
- HE 57. Junco [hyemalis]. The genus Junco comprises a single superspecies, consisting of J. hyemalis, J. phaeonotus, and Costa Rican J. vulcani (Mayr, 1942). J. hyemalis includes morphologically very divergent groups of races which hybridize in secondary contacts wherever they meet. Miller (1941) discussed variation among all forms now included in this superspecies, but he considered hyemalis, oreganus, caniceps, aikeni, and insularis (Guadalupe Island) as separate species. The lumping of all "darkeyed" juncos into hyemalis, suggested by Mayr (1942), has been discussed and followed by Dickinson (1953), Phillips (1961), and Short (1969a). Southern Baja California bairdi was shown by Miller (1941) to be related to J. phaeonotus, with which it is here considered conspecific. Middle American alticola is also a distinctive race of phaeonotus, which does not come into contact with J. hyemalis in the breeding season, although their ranges approximate each other in Arizona (Phillips, in Phillips, et al.,

- 1964). The latter author discussed some of the races of *J. hyemalis. J. vulcani* exhibits some features of the zonotrichine sparrows (Short, pers. obser.).
- HE 58. Calcarius mccownii. We follow Sibley and Pettingill (1955) in merging Rhynchophanes (1858) in Calcarius (1802). Its relationships are uncertain but probably lie with the lapponicus-ornatus group. It has hybridized with C. lapponicus (Sibley and Pettingill, 1955).
- HE 59. Calcarius lapponicus. There is weak racial differentiation in this longspur (Vaurie, 1956c). Allopatric C. ornatus is somewhat similar and may comprise a superspecies with lapponicus, but further information is needed concerning longspur relationships.
- HE 61. Calcarius pictus. This distinctive species may be more closely related to species of *Emberiza* than to other longspurs (Jehl, 1968a).
- HE 62. Plectrophenax nivalis. Variation in nivalis has been discussed by Salomonsen (1950) and by Vaurie (1956c). Insular hyperboreus is regarded by us as a well-marked subspecies of nivalis it is sometimes considered specifically distinct. Sealy (1969) has recently discussed its status and the interbreeding of nivalis and hyperboreus. Apparently individuals of the latter somewhat frequently occur outside of Hall and St. Matthews islands (where nivalis does not occur), there to interbreed with, and defend territories against, individuals of nivalis. Some introgression is suggested by Sealy's discussion. Further studies of the status of hyperboreus are needed. This genus is doubtfully distinct from Emberiza, but studies of old World buntings are needed to establish its relationships to species of that genus.

## IV

## **DISCUSSION AND CONCLUSIONS**

## PROBLEMS OF SPECIES DELIMITATION

Four classes of phenomena may cause difficulties for the avian taxonomist attempting to delimit species. These are: (a) whether or not certain sympatric individuals are members of the same species (classes 1 and 2 below); and (b) whether or not certain, usually allopatric, populations have attained species level (classes 3 and 4 below). The plant taxonomist (Grant, 1957) and the student of various groups of invertebrates (Mayr, 1957) have some additional classes of difficulties (e.g., uniparental reproduction, polyploidy, host races) with which the ornithologist is not concerned.

### 1. POLYMORPHISM

Different phena (= morphs, forms, varieties) of a species are sometimes so different that they are at first described as different species. The occurrence of two or more morphs in a single species is a common phenomenon in many groups of animals, particularly in snails, insects, and various groups of marine invertebrates. This has been the cause of much taxonomic confusion. Intraspecific morphs also occur in birds, and Stresemann, especially, has pointed out in his *Mutationsstudien* (1923-1926) that many (indeed well over one hundred) described species of birds are invalid because they are nothing but morphs of other species.

Polymorphism has not been a major source of confusion in the delimitation or recognition of North American birds for more than one hundred years, except in about four species (see below). For the sake of discussion it is important to distinguish two kinds of polymorphism: (a) scattered polymorphism, occurring at variable frequencies in many, if not all, populations of the species; (b) polymorphism in zones of secondary intergradation (hybridization) between drastically different subspecies (which may or may not be completely monomorphic).

(a) Scattered polymorphism is found in a number of species. For example, it occurs in Aechmophorus, several heron genera, several genera of hawks, and in Bonasa, Haematopus, Uria, Otus, Junco, and other genera (some are mentioned in the taxonomic comments). Few of these cases have presented problems of discrimination in recent decades, and as a group they have offered no greater problems to taxonomists than those due to age, seasonal, and sexual differences. The latter are a source of much uncertainty in the taxonomy of many animal groups, and early ornithology had its share of this category of difficulties, such as when Linnaeus considered male and female Mallards, or juvenal and adult Goshawks, as separate species. The plumage sequence of certain species

of herons, such as the Little Blue Heron, confused ornithologists of the nineteenth century, but these and all other difficulties caused by individual variation ceased to be of taxonomic significance more than one hundred years ago.

(b) In a limited number of cases entire populations of a species may contain but one morph, while other populations of this species have either another morph or both morphs present; in other words, the polymorphism is geographically oriented. Usually in such cases a polymorphic population occurs between two largely monomorphic populations. The best known instances of this type in North America are Ardea cinerea (AF 12), Anser caerulescens (AI 7), and Psaltriparus minimus (GD 8). A previous geographic isolation and recent hybridization between subspecies is evident. (Buteo jamaicensis-"harlani" may also belong here, but needs further study.) Additional cases of polymorphism due to hybridization may prove to occur within North America (e.g., possibly Branta bernicla-"nigricans," Haematopus ostralegus-"bachmani," and Charadrius hiaticula-"semipalmatus"). Sporophila torqueola displays polymorphism due to hybridization outside North America.

The occurrence of polymorphism in such hybrid populations indicates that the subspecies involved in the hybridization had acquired monogenic or oligogenic differences in certain color characters with typical Mendelian segregation resulting from the hybridization. Cooke and Cooch (1968) have demonstrated this excellently for *Anser caerulescens*. The drastic visual, but fundamentally superficial, difference between the parental subspecies (Blue Goose-Snow Goose; Great White Heron-Great Blue Heron) is, of course, no reason for specific separation.

We see that polymorphism has been troublesome in the taxonomy of less than 1% of North American avian species. It is precisely the biological species concept which has helped in the elucidation of these problems, particularly in the cases of the Snow Goose-Blue Goose, and the Great White Heron-Great Blue Heron. This again demonstrates its extreme usefulness in resolving difficult situations.

# 2. PHENOTYPIC SIMILARITY OF SPECIES

Species that are morphologically indistinguishable, or at least so similar that they are at first overlooked (= sibling species), are a major source of difficulty in most branches of animal taxonomy. Among insects the sibling species of Drosophila, Anopheles, and crickets are legion, but they are also frequent in other groups of insects, among anurans (Rana, Hyla), and in mammals. In comparison with the high frequency of sibling species in other groups of organisms, sibling species are remarkably rare in birds. Except for the tyrant flycatchers (Empidonax, Elaenia, Myiarchus, etc.) and swifts (Apus, Collocalia), they are limited to a few scattered genera. The reason for the rarity of sibling species among birds is presumably because the intraspecific recognition signals of birds

(coloration, calls, and songs) invoke the very two sense organs (eye and ear) that are man's principal senses. Where "species recognition" and courtship stimuli make major use of chemical signals, as in mammals, insects, and lower invertebrates, man with his poor sense of smell (and even poorer other chemical senses) is rather helpless. Most morphological sibling species in these groups well may have conspicuous species characters of a chemical nature, which are indiscernible by us. The superficial similarity of some species (e.g., resemblance of species of *Dryocopus* to species of *Campephilus*), due to social mimicry (Moynihan, 1968) or other factors resulting in convergence or parallelism, is not a problem for taxonomists, although field identification of such species may present problems.

When we consider sibling species of birds from the point of view of the difficulty they have caused for the ornithologist in his task of delimiting species, we see at once that they fall into two groups: (A) sympatric sibling species; (B) members of the same superspecies, with or without slight overlap and with or without occasional hybridization.

## A. Sympatric Sibling Species

Non-Passeres. These avian orders contain remarkably few sibling species. There is, of course, considerable arbitrariness in deciding what to include. For instance, Sterna hirundo 1758 and Sterna paradisaea 1763 appear rather similar to the beginner, but were first distinguished more than 200 years ago and are really very different when studied closely. Forster's Tern (forsteri 1834) and the Roseate Tern (dougallii 1813) are in the same category, and can hardly be considered sibling species.

The Semipalmated Sandpiper (Calidris pusillus 1766) and Western Sandpiper (C. mauri 1856) might qualify; there is little doubt that the similarity of mauri to pusillus prevented it from being described any earlier. Otus trichopsis (1832), as distinct from the sympatric races of Otus asio, is another candidate for this category. In spite of its early description it was confused by ornithologists until about 1890.

Thus, it is evident that there are essentially no good sympatric sibling species among the North American Non-Passeres.

Passeres. Sibling species are more frequent among the Passeres. Anyone who has attempted to identify migrating empidonax flycatchers in the fall, when they are not singing, would presumably be willing to designate our four eastern species of *Empidonax* as sibling species, despite the fact that *virescens* 1810\* (1818), *traillii* 1831, *minimus* 1843, and *flaviventris* 1843 are easily distinguishable in the spring when they are singing. The same is true of some western species of *Empidonax*, for instance *wrightii* 1858 and *oberholseri* 1889\* (1939). For other sibling species of flycatchers see below under "B".

Swainson's Thrush (Catharus ustulatus 1840) and the Gray-cheeked

<sup>\*</sup>Year of recognition as species. Date of valid name given in parentheses.

Thrush (*C. minimus* 1848) are certainly rather similar, although their differentiation has not been a problem for more than a hundred years. The same is true for the Purple Finch (*Carpodacus purpureus* 1789) and Cassin's Finch (*C. cassinii* 1854), and for the Clay-colored Sparrow (*Spizella pallida* 1830) and Brewer's Sparrow (*S. breweri* 1856).

Again, as with the Non-Passeres, truly sympatric sibling species among the North American Passeres have not been a problem for the bird taxonomists for more than 100 years, with the single exception of some members of the genus *Empidonax*.

## B. Sibling Species that are Members of the Same Superspecies

There are numerous species in this category and many have caused difficulties for the avian taxonomist. Curiously, in most cases the difficulty was not one of recognition but rather of ranking. A look at the dates of their description demonstrates how early most of them were recognized. So early, indeed, that most of them were originally designated with a binomen, as was any taxonomically recognizable population in those days. But, at a later period, when avian taxa were gathered into polytypic species, these sibling species were often reduced to the rank of subspecies; indeed for many of them there is still no unanimity among bird taxonomists as to whether they should be treated as subspecies or as species (= allospecies in a superspecies). In migration and winter some of these allopatric sibling species overlap broadly. Since they are nonvocal at this season, they often present problems of identification in the field and occasionally even in hand (Contopus, Empidonax).

The listing of this group of sibling species, as given below, is somewhat arbitrary, just as above under "A." However, we hope that we have succeeded in including all the more relevant cases.

## Non-Passeres

Arctic Loon (Gavia arctica 1758) — Pacific Loon (pacifica 1858)

Greater Scaup (Aythya marila 1761) — Lesser Scaup (affinis 1838)

Short-billed Dowitcher (Limnodromus griseus 1789) — Long-billed Dowitcher (scolopaceus 1823)

Herring Gull (Larus argentatus 1763) — Kumlien's Gull (L. glaucoides kumlieni 1883) — Thayer's Gull (L. g. thayeri 1915)

Chimney Swift (Chaetura pelagica 1758) — Vaux's Swift (vauxi 1839)

#### Passeres.

Tropical Kingbird (Tyrannus melancholicus 1819) — Couch's Kingbird (couchii 1858)

Great Crested Flycatcher (Myiarchus crinitus 1758) — Wied's Crested Flycatcher (tyrannulus cooperi 1858)

- Traill's Flycatcher (*Empidonax traillii* 1828) Alder Flycatcher (*alnorum* 1895)
- Least Flycatcher (Empidonax minimus 1843) Hammond's Flycatcher (hammondii 1858)
- Eastern Wood Pewee (Contopus virens 1766) Western Wood Pewee (sordidulus 1859)
- Black-capped Chickadee (*Parus atricapillus* 1766) Carolina Chickadee (*carolinensis* 1834)
- Eastern Meadowlark (Sturnella magna 1758) Western Meadowlark (neglecta 1834)
- Boat-tailed Grackle (Quiscalus mexicanus 1788) Great-tailed Grackle (major 1819)
- Common Redpoll (Acanthis flammea 1758) Hoary Redpoll (hornemanni 1843)

This category thus contains five sets of Non-Passeres and nine sets of Passeres in which the component species are largely or entirely allopatric and do not interbreed in the zone of contact or do so only sparingly (or locally). Of the 29 sibling species involved in these 14 sets, 26 were described more than 100 years ago; the exceptions are one empidonax (1895) and two arctic gulls (1883, 1915).

Some taxonomists may well add to this list a few taxa which we list in our tabulation under "C" (strongly differentiated polytypic species). No one questions that some polytypic species taxa form borderline cases, as one must expect as a consequence of evolution.

Even if such additional borderline cases were added, it would not change our basic conclusion that sibling species are a rare phenomenon in birds, as compared with other groups of organisms. In perhaps no other category of taxonomic difficulties has the biological species concept been as helpful as in the ranking of taxa that are sibling species.

## 3. HYBRIDIZATION

Hybridization causes three kinds of difficulties for plant and animal taxonomists:

(a) An interspecific hybrid has such distinct, indeed unique features, that is is described as a separate species. This occurs frequently in plant taxonomy but is not a major source of difficulty in bird taxonomy. A number of names have been proposed for such bird hybrids, particularly among hummingbirds and wood warblers, but their hybrid nature was usually soon established without leading to controversy. The latest name is Dendroica potomac (1940), given to a hybrid between the Parula and Yellow-throated warblers. Its hybrid nature was suspected even before it was formally described. No species listed in the A.O.U. Check-list (1957) conceivably could be a hybrid between two (other) species, nor has any species of the 1931 Check-list since been found to be a hybrid.

- (b) Two (in other respects) good sympatric species which hybridize to such an extent and show so much introgression that, with equal justification, they might be considered a single species. The six species pairs listed below under Category "C" are potential candidates for this category, but none of them truly qualifies. Even the Prairie Chicken and Sharptailed Grouse, a species pair showing a good deal of local hybridization, maintain their specific discreteness to such an extent that no one has ever suggested merging them into a single species. One case outside of North America, but involving a North American species, clearly qualifies here. That is the hybridization between Pipilo erythrophthalmus and P. ocai in Mexico. This is the only case in which the present authors differ in their evaluation of North American species taxa. Short considers them as conspecific and Mayr considers them as two species. This is the only instance among North American birds where hybridization causes difficulties for the biological (or for that matter, any other) species concept.
- (c) Two species taxa hybridize in a zone of contact or secondary hybridization. In these cases the biological species concept has been of great help. It permitted the development of clear-cut criteria of ranking (Short, 1969a). When hybridization is limited owing to an evident mating preference for conspecific mates, the taxa are considered allospecies within a superspecies (Category "B" of the list below). When there is indiscriminate pairing and massive introgression, the two taxa are considered subspecies of a single polytypic species (Category "A").

Hybridization under natural conditions has affected at least 52 species and superspecies (10% of a total of 516 non-marine species and superspecies) within North America; excluded from consideration are unique instances of hybridization (see lists of Cockrum, 1952; Gray, 1958). Most of these species are widespread within North America and the bulk of them extend outside of the continent to Middle America (or even South America) or Eurasia and beyond. Likewise, it is significant that a majority of the species involved are considered biologically successful in terms of their abundance; they include no rare species, and, indeed, many, such as mallards, flickers, house wrens, orioles, towhees, and juncos, are among the most familiar of North American birds. These instances of hybridization may be categorized as follows:

### A. Intraspecific Hybridization

hynchos (platyrhynchos, diazi groups), Dendragapus obscurus (obscurus, fuliginosus groups), Dendragapus canadensis (canadensis, franklinii groups), Colaptes auratus (auratus, cafer groups), Colaptes auratus (cafer, chrysoides groups), Perisoreus canadensis (canadensis, obscurus groups), Parus bicolor (bicolor, atricristatus groups), Psaltriparus minimus (minimus, plumbeus groups), Troglodytes aedon (aedon, brunneicollis groups), Dendroica coronata (coronata, auduboni groups), Quiscalus quiscula

(quiscula, versicolor groups), Icterus galbula (galbula, bullockii groups), Leucosticte arctoa (tephrocotis, atrata groups), Pipilo erythrophthalmus (erythrophthalmus, alleni groups), Pipilo erythrophthalmus (maculatus, erythrophthalmus groups), Pipilo fuscus (crissalis, mesoleucus groups), Aimophila belli (belli, nevadensis groups), Junco hyemalis (hyemalis, oreganus groups), and Junco hyemalis (oreganus, caniceps groups).

- β Extent of hybridization limited or uncertain 7 situations: Branta canadensis (canadensis, hutchinsii groups), Branta bernicla (bernicla, nigricans groups), Anas crecca (crecca, carolinensis groups), Otus asio (asio, kennicotti groups), Corvus brachyrhynchos (brachyrhynchos, caurinus groups), Oporornis philadelphia (philadelphia, tolmiei groups), and Carduelis psaltria (psaltria, hesperophilus groups).
- γ Polymorphism 3 or 4 situations (see section on polymorphism): Ardea cinerea ("occidentalis" morph, wardi), Anser caerulescens ("hyperboreus" morph, caerulescens), Buteo jamaicensis ("harlani" morph, calurus)?, Psaltriparus minimus ("melanotis" morph, plumbeus). (Possibly also Charadrius hiaticula, presently in Category "B".)

# B. Interspecific Hybridization between Largely Allopatric Members of the Same Superspecies

- α Zones of overlap and extensive hybridization 5 situations: Anas [platyrhynchos] (A. platyrhynchos, A. rubripes), Larus [argentatus] (L. argentatus, L. glaucescens), Vermivora [pinus] (V. pinus, V. chrysoptera), Pheucticus [ludovicianus] (P. ludovicianus, P. melanocephalus), and Passerina [cyanea] (P. cyanea, P. amoena).
- β Limited hybridization in contact or overlap zone 13 situations involving 12 superspecies: Gavia [arctica] (G. arctica, G. pacifica), Callipepla [californica] (C. californica, C. gambelii), Rallus [longirostris] (R. longirostris, R. elegans), Charadrius [hiaticula] (C. hiaticula, C. semipalmatus), Picoides [scalaris] (P. scalaris, P. nuttallii), Sphyrapicus [varius] (S. varius, S. nuchalis), Contopus [virens] (C. virens, C. sordidulus), Parus [atricapillus] (P. atricapillus, P. carolinensis), Dendroica [virens] (D. occidentalis, D. townsendi), Sturnella [magna] (S. magna, S. neglecta), Piranga [olivacea] (P. olivacea, P. ludoviciana), and Acanthis [flammea] (A. flammea, A. hornemanni).

# C. Limited Hybridization between Sympatric Species Not Belonging to the Same Superspecies — 6 Situations

Tympanuchus cupido X T. phasianellus, Callipepla gambelii X C. squamata, Archilochus alexandri X A. costae, Archilochus anna X Selasphorus sasin, Picoides nuttallii X P. pubescens, and Zonotrichia albicollis X Junco hyemalis.

The categories utilized above and various terms (Hybrid Zone, Zone

of Overlap and Hybridization) are discussed and defined in Short (1969a). Some of the species listed above, such as Anas platyrhynchos and Pipilo erythrophthalmus, also engage in hybridization in situations outside of North America. Other North American species, perhaps numbering 12 or 15 beyond those included above, hybridize elsewhere in the world, but not in North America (e.g., intraspecific hybridization among forms of Cyanocitta stelleri, Motacilla flava, Luscinia svecica, Mimus polyglottos, and Agelaius phoeniceus; hybridization between species of the superspecies Butorides [virescens], Fulica [atra], Tyrannus [melancholicus] and Progne [subis], and between species in the genera Pluvialis and Cynanthus).

As mentioned previously, some instances of hybridization pose difficult taxonomic problems and a very large number are in need of study or further study. This is particularly true of situations in categories  $A_{\beta}$  (Branta canadensis, for instance),  $A_{\gamma}$  (especially Buteo "harlani") and  $B_{\beta}$  (e.g., the Sphyrapicus varius — S. nuchalis situation). An additional situation at present under study (interaction between Empidonax traillii and E. alnorum) may prove to involve hybridization. There are doubtless a few other cases involving limited interspecific hybridization and perhaps narrow hybrid zones (intraspecific hybridization) remaining to be discovered.

An analysis of the distribution and history of hybrid situations and avian secondary contact zones in North America will be presented elsewhere (Short, MS).

It would appear that backcrossing occurs in hybrid situations involving at least 35 of the 52 species and superspecies listed above. We consider hybridization to be a significant factor affecting the recent evolution of these 35 species. Although this involves only a minor portion of the North American avifauna, the prominence in the avifauna of most of the species involved renders their hybridization of considerable evolutionary consequence. Nearly one-third (12) of the cases in which hybridization is significant involve Non-Passerine species; these species are involved in 40% of all instances of intraspecific hybridization and 60% of the instances of interspecific hybridization. Hybridization is especially prevalent in the Anatidae, Tetraonidae, and Picidae among the Non-Passerines, and in the nine-primaried Oscines (especially Parulidae, Icteridae, and Fringillidae) among the Passeriformes.

Hybridization appears not to be a significant factor in the evolution of 17 of the species and superspecies which hybridize but are not known to backcross (although some may prove to do so). Of course these may have hybridized to a greater extent at some time in the past. The 17 include: Branta canadensis (category  $A_{\beta}$ ), Branta bernicla ( $A_{\beta}$ ) Anas crecca ( $A_{\beta}$ ), Otus asio ( $A_{\beta}$ ), Gavia [arctica] ( $B_{\beta}$ ), Callipepla [californica] ( $B_{\beta}$ ), Rallus [longirostris] ( $B_{\beta}$ ), Sphyrapicus [varius] ( $B_{\beta}$ ), two situations involving three species), Dendroica [virens] ( $B_{\beta}$ ),

Sturnella [magna] (B $\beta$ ), Piranga [olivacea] (B $\beta$ ), Archilochus alexandri  $\times$  A. costae (C), Archilochus anna  $\times$  Selasphorus sasin (C), Picoides nuttallii  $\times$  P. pubescens (C), Zonotrichia albicollis  $\times$  Junco hyemalis (C), and probably Callipepla gambelii  $\times$  C. squamata (C; one purported backcross hybrid cited above). Further study of many of these situations is desirable especially of those in category A $\beta$ . Interbreeding forms of the latter are treated tentatively (by various taxonomists, including us) as subspecies for reasons already mentioned, but new data concerning them are vital for a full understanding of these situations.

Instances in category  $A_{\gamma}$  (polymorphism) involve hybridization, but they are discussed in another section.

## 4. EVOLUTIONARY INTERMEDIACY

Most species vary in space and time, consisting of numerous populations which differ from each other to a greater or lesser degree. The taxonomist recognizes polytypic species in order to cope with the multidimensional distribution of populations and taxa. The assignment of populations and taxa near the species level to the proper polytypic species often creates difficulties. When a geographic isolate is clearly distinct from populations of the most closely related species it is often uncertain whether or not it has fully attained the species level. The existence of such borderline cases, or "semispecies" (Short, 1969a), is an inevitable consequence of geographic speciation. There is rarely unanimity among bird taxonomists concerning the treatment of these cases. Some, particularly those who stress morphological criteria, will tend to call them species. Others who remember the strong differences among some freely interbreeding subspecies, tend to rank them as subspecies. On the whole we favor the latter alternative. The criteria on which to base inferences concerning ranking in such situations are discussed in detail by Mayr (1969). It is of interest to record the frequency of such borderline cases, which are tabulated in Tables 2-5.

## A. Species Polytypic in Their North American Range

Let us first restrict ourselves to an examination of the species within their North American ranges only (Tables 2 and 3). Monotypic species (Column A) number 360 out of a total of 607 species (= 59.2%). There is considerable difference among the various groups of families. Groups A (80.3%), F (79.4%), and C (78.0%) show a higher percentage of monotypic species than do marine birds (70.0%), and all of these groups show percentages greater than the total mean value (59.2%). Families of the G group of Passerines (mainly with Old World relationships) have the lowest percentage of monotypic species within North America (38.4%). Groups A, B, and C are admittedly somewhat arbitrary assemblages, but there is no justification for analyzing each family individually when one considers that most families range widely beyond the limits of North America (as represented in this tabulation).

TABLE 2

NUMBER OF MONOTYPIC AND POLYTYPIC SPECIES BASED
ON THEIR NORTH AMERICAN RANGE ONLY<sup>1</sup>

| Group  | Total | Category |     |    |  |  |
|--------|-------|----------|-----|----|--|--|
| -      |       | Α        | B   | C  |  |  |
| Marine | 40    | 28       | 11  | 1  |  |  |
| Α      | 77    | 62       | 9   | 6  |  |  |
| В      | 51    | 25       | 20  | 6  |  |  |
| C      | 86    | 67       | 18  | 1  |  |  |
| D      | 16    | 10       | 6   | 0  |  |  |
| E      | 66    | 31       | 31  | 4  |  |  |
| F      | 34    | 27       | 7   | 0  |  |  |
| G      | 86    | 33       | 45  | 8  |  |  |
| H      | 151   | 77       | 54  | 20 |  |  |
|        |       | 45-      |     |    |  |  |
| Total  | 607   | 360      | 201 | 46 |  |  |

<sup>&</sup>lt;sup>1</sup>See Table 3 for percentages based on these numbers. The categories are those listed in the analytical table (Table 1).

TABLE 3

PERCENT OF MONOTYPIC AND POLYTYPIC SPECIES BASED ON THEIR NORTH AMERICAN RANGE ONLY<sup>1</sup>

| Group        | ${ m T}$ | Total   |      | Category     |       |              |  |
|--------------|----------|---------|------|--------------|-------|--------------|--|
| _            | No.      | Percent | Α    | В            | A+B   | C            |  |
| Marine       | 40       | 100     | 70.0 | 27.5         | 97.5  | 2.5          |  |
| Α            | 77       | 100     | 80.3 | 11.8         | 92.1  | 7.9          |  |
| В            | 51       | 100     | 49.0 | 39.2         | 88.2  | 11.8         |  |
| C            | 86       | 100     | 78.0 | 20.8         | 98.8  | 1.2          |  |
| D            | 16       | 100     | 62.5 | 37.5         | 100.0 | 0.0          |  |
| ${f E}$      | 66       | 100     | 47.0 | 46.9         | 93.9  | 6.1          |  |
| ${f F}$      | 34       | 100     | 79.4 | 20.6         | 100.0 | 0.0          |  |
| G            | 86       | 100     | 38.4 | 52.5         | 90.9  | 9.1          |  |
| $\mathbf{H}$ | 151      | 100     | 51.0 | <b>35.</b> 7 | 86.7  | 13.3         |  |
|              | ,        |         |      |              |       |              |  |
| Total        | 607      | 100     | 59.2 | 33.2         | 92.4  | 7 <b>.</b> 6 |  |

<sup>&</sup>lt;sup>1</sup>For numbers on which these are based see Table 2. The categories are those listed in the analytical table (Table 1).

Species in Column B are uncomplicated polytypic species not causing difficulties for species delimitation. Of the 607 species, 201 or almost exactly one third (33.2%) are not exceptional. On the whole those families exhibiting a high percent of monotypic species show a low percent of uncomplicated polytypic species (Column B) and vice versa. Within each of the nine groups from marine species to Group E, the combined percentages of Columns A and B vary only between 86.7% and 100.0%.

Column C contains the most interesting statistics of this tabulation. This lists the 46 species (among 607) which are strongly differentiated polytypic species. Each of these contains at least one population (mainly peripherally isolated) which we rank as subspecies but which some other

taxonomists consider, or have in the recent past considered, sufficiently distinct to be ranked as full species. The nine-primaried Oscines (13.3%) and Group B (hawks, gallinaceous birds; 11.8%) include the greatest number of such species.

The total of strongly differentiated polytypic species in North America is remarkably low. One must remember, however, that the average geographic range of a bird species is very great, and that these ranges often extend well beyond North America (as defined above). Indeed, when we tabulate (Tables 4 and 5) the kinds of species taking into account their entire ranges (world-wide!), the percent showing difficulties (Column C) becomes much bigger.

TABLE 4

NUMBER OF MONOTYPIC AND POLYTYPIC SPECIES BASED
ON THEIR WORLD-WIDE RANGE<sup>1</sup>

| Group        | Total | Category |             |     |
|--------------|-------|----------|-------------|-----|
| _            |       | Α        | B           | C   |
| Marine       | 40    | 15       | 21          | 4   |
| Α            | 77    | 35       | 28          | 14  |
| В            | 51    | 8        | 30          | 13  |
| C            | 86    | 51       | 28          | 7   |
| D            | 16    | 5        | 7           | 4   |
| ${f E}$      | 66    | 13       | 36          | 17  |
| $\mathbf{F}$ | 34    | 17       | 13          | 4   |
| G            | 86    | 13       | 48          | 25  |
| H            | 151   | 61       | 53          | 37  |
|              |       |          | <del></del> |     |
| Total        | 607   | 218      | 264         | 125 |

<sup>&</sup>lt;sup>1</sup>See Table 5 for percentages based on these values. The categories are those listed in the analytical table (Table 1).

TABLE 5
PERCENT OF MONOTYPIC AND POLYTYPIC SPECIES BASED
ON THEIR WORLD-WIDE RANGE<sup>1</sup>

| Group        | Total |         |      |             |      |      |
|--------------|-------|---------|------|-------------|------|------|
| <u> </u>     | No.   | Percent | Α    | Catego<br>B | A+B  | C    |
| Marine       | 40    | 100     | 37.5 | 52.5        | 90.0 | 10.0 |
| Α            | 77    | 100     | 44.7 | 36.9        | 81.6 | 18.4 |
| ${f B}$      | 51    | 100     | 15.7 | 58.8        | 74.5 | 25.5 |
| C            | 86    | 100     | 59.3 | 32.6        | 91.9 | 8.1  |
| D            | 16    | 100     | 31.2 | 43.8        | 75.0 | 25.0 |
| E            | 66    | 100     | 20.0 | 54.2        | 74.2 | 25.8 |
| $\mathbf{F}$ | 34    | 100     | 50.0 | 38.2        | 88.2 | 11.8 |
| G            | 86    | 100     | 15.1 | 55.8        | 70.9 | 29.1 |
| H            | 151   | 100     | 40.4 | 35.1        | 75.5 | 24.5 |
|              |       |         |      |             |      |      |
| Total        | 607   | 100     | 35.8 | 43.6        | 79.4 | 20.6 |
|              |       |         |      |             |      |      |

<sup>&</sup>lt;sup>1</sup>For numbers on which these are based see Table 4. The categories are those listed in the analytical table (Table 1).

## B. ENDEMIC SPECIES

The number of species endemic to North America as we have defined the area is relatively small. The more northerly species and the marine birds tend to range into Asia, and the more southerly species range into Mexico, Central America and the West Indies. Altogether 189 of the 607 species (= 31.2%) are endemic, confined to North America as breeding birds. Only three of the 40 seabirds (one gull, two auks) are endemic while 73, or almost half, of the 151 nine-primaried Oscines are endemic. The high value for the latter group probably reflects the fact that some of the families originated in or just to the south of North America as we have defined it, and their radiation has taken place partly within North America (Mayr, 1946). Endemism is particularly high among the wood warblers and emberizine finches.

# C. Species Polytypic in Their World-Wide Range

As might be expected, the more distant isolates are from each other, the more distinct they tend to be. The percentage of strongly differentiated polytypic species is almost three times as high (20.6% vs. 7.6%) when the world range is considered as when only their North American range is considered. Groups B, D, and E among Non-Passeres and both groups (G, H) of Oscines show particularly high percentages, although the percentage of strongly differentiated species does not exceed 29.1% in any family.

Monotypic species account for as many as 217 (35.8%) of the 607 species, even when considered on a world-wide basis; they amount to 59.2% for North America alone. The shorebirds and their relatives (Group C) are particularly rich in monotypic species (59.3%), while tyrant flycatchers and their relatives (Group F) are a close second (50.0%). The reasons for the low level of visible geographic variation in the two groups are, however, presumably quite different. Many tyrant flycatchers have local species ranges, and display little plumage variation, as indicated by the frequency of sibling species in this group. The shorebird group (also including gulls, rails, etc.) contains many widespread and highly migratory species in which gene flow is great, thus limiting strong differentiation.

Combining Columns A and B to include those species presenting no difficulties of species delimitation gives 481 (79.4%) of the 607 species. The remaining 126 species, or about one-fifth of the total, contain isolates which we consider to represent very well defined subspecies, while certain other authors have treated various of them as full species.

The findings shown in Tables 2-5 from the point of view of difficulties presented by problems in species delimitation may be briefly summarized as follows. Geographic variation occasionally causes enough evolutionary intermediacy to become a major source of difficulty. This is no problem at all for those who work with species as ecologists or ethologists, who are concerned with the interaction of species in a local situation — evolutionary intermediacy produced by geographic variation is then lacking and poses no problem. Since birds have very wide distributions, strongly differentiated polytypic species are only a minor problem (involving 7.6% of the total) even taking all of North America into consideration. Major problems are presented only when we consider the 607 species of North American birds from a world-wide viewpoint, and then the species with difficulties of delimitation come to comprise one-fifth (20.6%) of the total.

#### D. Superspecies

Incipient species that have not yet crossed the threshold of species status are one group of taxa reflecting evolutionary intermediacy. Superspecies, that is, groups of taxa which have barely crossed this threshold, are another such group. Which groups of allopatric species taxa to designate as strongly differentiated polytypic species (Column C) and which others as superspecies (Column D) is often subject to a somewhat arbitrary decision (indeed, where we lack sufficient knowledge on which to base a firm decision, as within the genera *Elanus* and *Ortalis*, the decision may involve also Category E, the species group). In continental areas this difficulty is reduced because the allospecies of which the superspecies is composed meet parapatrically (with no or only limited interbreeding) or even overlap slightly. In a majority of cases there is a consensus concerning which taxa should be recognized as species but combined into superspecies.

The high frequency of superspecies in insular regions has been known ever since Rensch (1929) first called attention to it. That superspecies are common on continents has been discovered only rather recently. This emphasizes the need for a continent-wide and even world-wide approach to obtain the relevant information. Also, species have to be recorded as zoogeographic species (see above) for any analysis.

TABLE 6
FREQUENCY OF SUPERSPECIES IN NORTH AMERICA<sup>1</sup>

| Group        | Zoogeographic | North America Only |                  | World-wide Range |                  |
|--------------|---------------|--------------------|------------------|------------------|------------------|
|              | Species       | Superspecies       | Other<br>Species | Superspecies     | Other<br>Species |
| Α            | 72            | 5                  | 67               | 19               | 53               |
| В            | 49            | 2                  | 47               | 16               | 33               |
| C            | 81            | 5                  | 76               | 18               | 63               |
| D            | 16            | 0                  | 16               | 4                | 12               |
| E            | 57            | 6                  | 51               | 19               | 38               |
| $\mathbf{F}$ | 29            | 5                  | 24               | 9                | 20               |
| G            | 78            | 7                  | 71               | 21               | 57               |
| Н            | 135           | 14                 | 121              | 21               | 114              |
|              |               |                    |                  | <del></del>      |                  |
| Total        | 517           | 44                 | 473              | 127              | 390              |

<sup>&</sup>lt;sup>1</sup>See text for zoogeographic species, which include superspecies and other species (which are simply those species not comprising part of a superspecies).

Marine birds are especially poor in superspecies (two among 38 zoogeographic species in North America), and usually are not included in regional analyses of superspecies. They are omitted from Table 6 which treats North American superspecies.

Of the 517 zoogeographic species, 44 are superspecies represented by more than one species within North America (the 44 include 94 species), and 83 others are the sole species representing their superspecies within North America. Altogether 127 of the 517 zoogeographic species belong to superspecies and 391 do not. Thus, almost one-quarter (24.4%) of the zoogeographic species represent superspecies. The total number of non-marine breeding species in North America is 567, and of these species 176, or about 31%, belong to superspecies.

The number of superspecies varies among the taxonomic groups. Of the larger Non-Passerines (Groups A, B, C, D) only 12 of the 217 species, or 5.5%, belong to North American superspecies, while among owls, hummingbirds, woodpeckers (Group E), and Passerines (Groups F, G, H), 10.7% are members of superspecies; all four of the latter groups individually score high (Table 2). However, the situation is quite different when it comes to membership in a superspecies on a world-wide basis. Here, the large Non-Passerines score as high (22-33%) as the Passeres; indeed the nine-primaried Oscines are, of course, essentially New World in distribution, and component species of their superspecies tend to occur entirely within North America, or just to the south, while Non-Passerine species of superspecies have related elements of their superspecies in the Holarctic as frequently (or more so) as in the Neotropics.

In northern Melanesia, 39 (28.3%) of 177 zoogeographic species (except seabirds) are superspecies. If we exclude waterbirds (mostly Group A) from the North American list, 445 species are left among which 108 (32.0%) are superspecies (on a world-wide basis). The percentage of superspecies is, thus, even higher in North America than in Melanesia. For Africa, Hall and Moreau (1970) found an equally high prevalence of superspecies. Among 25 families (or subfamilies) of African Passeres, they found that 486 (50.5%) of the 962 species belong to superspecies. Only 176 species are neither members of superspecies or species groups. In South America the number of superspecies is also large, as is evident from the analyses of Haffer (1969) and others.

The conclusion one can draw from this high frequency of superspecies is that newly evolved species frequently maintain a parapatric distribution pattern long after the geographic speciation is completed. It is presumably ecological factors (competitive exclusion; Mayr, 1969) which prevent these species from expanding widely into each other's ranges. Even though reproductive isolation has been perfected, ecological compatibility has not yet developed. Instances of parapatry and limited hybridization substantiate the fact that reproductive isolation of the species thus involved has occurred so recently that the terminal phases

of the speciation process are still progressing, and hence ecological compatibility has not yet had a chance to evolve. As a result, a certain amount of evolutionary intermediacy obtains, but it does not create any real difficulty for species delimitation.

TABLE 7
ZOOGEOGRAPHY OF NORTH AMERICAN SUPERSPECIES

| CATEGORY AND SUPERSPECIES                                                                                                                                                                                                                                                                                                                                                                                      | Non-<br>Passerine | Passerine | Total |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------|-----------|-------|
| I. North American endemics—EE 5, EH 13, FB 18, FB 19, HB 3, HB 15, HD 1, HE 56                                                                                                                                                                                                                                                                                                                                 | 2                 | 6         | 8     |
| II. New World endemics—AB 6, AD 1, AI 43, BB 3, BB 7, BB 13, BB 19, BE 1, BG 5, CC 1, DA 2, DA 3, DA 5, DC 2, EB 7, EB 8, EB 11, EB 16, EC 1, EC 2, ED 1, ED 2, EE 1, EE 9, EE 10, EH 1, EH 11, EH 17, FA 1, FB 3, FB 10, FB 11, FB 25, FB 26, FB 28, GB 3, GB 7, GC 10, GC 11, GD 6, GI 3, GI 5, GI 7, GK 3, GK 4, GN 3, HA 3, HA 9, HB 6, HB 13, HB 18, HC 2, HC 6, HE 15, HE 17, HE 19, HE 23, HE 26, HE 57 | 29                | 31        | 60    |
| III. Reach Eurasia or beyond, but not Central or South America—AA 1, AA 2, AI 14, AI 22, BD 2, CD 1, CE 1, CE 4, CE 7, CE 10, CE 12, CE 13, CE 17, CE 18, CE 20, GC 1, GC 7, GD 1, GD 3, GE 2, HE 5, HE 6                                                                                                                                                                                                      | 15                | 7         | 22    |
| IV. Reach both Eurasia and Central or South America—AB 3, AE 1, AF 1, AF 2, AF 3, AF 5, AF 10, AF 12, AH 1, AI 1, AI 17, AI 18, BB 1, BB 5, BB 6, BB 15, BB 21, BB 22, BD 4, BD 7, CC 2, CC 8, CD 3, CF 1, CF 2, CI 13, CI 20, EA 1, EB 3, EB 4, GA 1, GB 6, GC 8, GM 4, GQ 1, HE 1, HE 7                                                                                                                      | 30                | 7         | 37    |
| Total                                                                                                                                                                                                                                                                                                                                                                                                          | —<br>76           | 51        | 127   |

The zoogeographic relationship of the various superspecies is of considerable interest. Table 7 shows that the greatest number of superspecies are either New World endemics (60 + 8 = 68) or are wideranging (37). There are only 22 superspecies that reach Eurasia but not Central or South America.

### E. Species Group

An interesting category that is rarely involved in problems of evolutionary intermediacy is the species group. A natural outgrowth of the modern tendency to use the genus category (discussed below) to express relationship is that within a genus containing more than two species the relationships will differ in degree among these various species. Evolution of course dictates that differing degrees of relationship exist in larger genera, which may contain superspecies as well as more distantly related species. A group of closely related species (and superspecies) may form a discrete species group within a genus. It is a rather arbitrary decision as to how to designate such groups. We prefer to use the category of the subgenus for major distinct portions of a genus, and

species groups for minor but still distinct groups of species. The category of species groups is often strictly utilitarian, and the fewer species in the genus the less useful is the category.

Geographically isolated populations may diverge to the level of subspecies, and continue on to the species level (allospecies in a superspecies) or beyond. There are isolates which appear to be very distinct species, yet are obviously representative allopatric species. The genus *Scolopax* is a good example of a genus containing a group of isolates comprising a species group of this sort.

We have attempted to indicate species groups wherever possible (Column E), recognizing the species group as the next higher category of relationship for zoogeographical analyses. At the same time we recognize fully that the degree of relationship among species of many genera is largely unknown. Hence our listing for Column E is incomplete and tentative, and subject to considerable modification. It would be premature to analyze this category, and we include it chiefly for interest and in recognition of its relation to the superspecies and polytypic species categories.

A few facts about species groups are noteworthy. We have tabulated 33 instances in which we have some doubt as to whether the species involved comprise a superspecies or a species group (these cases are shown by connections between Columns D and E in Table 1). A majority (20) of these situations involve Non-Passeres, and the remaining 13 involve species of Passeres. In an additional four cases the taxa involved conceivably could comprise one strongly differentiated species, they could represent several species forming a superspecies (our preferred treatment), or, possibly, they could comprise a species group. These possibilities are shown on the chart by a connection from Column C through D to E. On the basis of the evidence available, we feel in each case (Elanus [caeruleus], BB 1; Falco [peregrinus], BD 4; Ortalis [vetula], BE 1; and Sterna [albifrons], CI 20) that the taxa involved are very closely related species comprising superspecies, but further studies are needed. Thus, only rarely and only on the basis of insufficient knowledge, is the category of the species group related to difficulties in species delimitation.

# REASONS WHY AVIAN SPECIES ARE WELL-DEFINED

The remarkably small number of cases in which the application of the biological species concept to avian taxa results in difficulties stands in considerable contrast not only to the situation in plants but also to that claimed for many groups of animals. Is this seeming difference spurious, in other words, is it merely an artifact of a backward state of taxonomy in most groups of animals, or is it indeed true that species are better defined in birds than in other groups of animals?

Unfortunately, it is too early to give a definitive answer to this question. This much, however, seems certain — there are some well-defined

differences between birds and other groups of animals. Let us mention some of them.

## 1. PHENOTYPIC DISTINCTNESS OF SPECIES

Sibling species exist in birds, both in North America (see above) and on other continents (Collocalia, Meliphaga, Elaenia), but are extremely rare when compared with the frequency of sibling species in anurans (Rana, Hyla), dipterans, orthopterans, and even mammals. Since signals for intraspecific communication in birds appeal to the same two sense organs (eye and ear) that are man's principal senses, and since chemical isolating mechanisms are apparently entirely absent, it is not surprising that bird species appear so conspicuously different to man. Sibling species are not a category of nature, but an artifact of the morphological analysis of preserved specimens, the normal taxonomic method. In groups of organisms where the selection pressure for the development and improvement of isolating mechanisms does not lead to a modification of the species-specific morphology, a phenotypic similarity of species may occur frequently.

### 2. PAIR FORMATION

Hybridization is one of the reasons for the poor definition of species borders in plants and some groups of animals. Pair formation and the more or less lengthy period of displays during the "engagement period," however, greatly reduce the probability of hybridization between individuals of different species of birds. There are few other groups of animals in which the pair bond is as firm and well secured as in most families of birds. The participation of the male in the raising of the young, characteristic of most species of birds, is another important factor in cementing — and continuously testing — the pair bond. This is the reason why hybridization between sympatric species of birds is apparently so much rarer than it is in other organisms.

#### 3. CHROMOSOMAL SPECIATION

Recent studies indicate that a certain amount of speciation in mammals is greatly helped by chromosomal rearrangement in small pheripherally isolated populations (Sorex, Mus, Spalax, Talpa, etc.) (references in Mayr, 1970). The same has been found for grasshoppers and seems widespread among insects. Alas, not nearly enough is known about avian chromosomes to state definitely whether or not similar phenomena occur in birds. However, at present there is no evidence that they do occur, nor do we know of any cases of incipient speciation in birds that would seem to demand an explanation by chromosomal rearrangement.

# 4. ECOLOGICAL SPECIATION

A parasitic or plant feeding species of insect or of other invertebrates (mites, nematodes, etc.) may be specialized for a single host species. In groups with host specificity it is often difficult to determine whether popu-

lations from different hosts are conspecific or not. Birds lack such extreme niche specialization and the problem of differentiating between ecological (host) races and species does not exist.

# RECENT TRENDS IN AVIAN CLASSIFICATION

## 1. CHANGES IN THE SPECIES CONCEPT

There has been frequent mention of how great a simplification in avian classification has been effected by the introduction of the polytypic species concept. It may be of interest to substantiate this with some concrete figures. Of the 607 species of birds breeding in North America, 389 are polytypic (Table 4). Within these 389 species no less than 315 North American subspecies were described initially as full species. Many others would have been described also under a binomen if the polytypic species concept had not been adopted by then.

These figures provide an effective answer to those who would like to abolish the category of the subspecies. To be sure, quite a few of the described subspecies are a result of the excessive splitting of clinal continuities. Most of these we could well do without, and indeed many are no longer recognized. However, the fact that so many local taxa originally were described as full species clearly shows that they represent taxa that should neither be suppressed, nor be designated as full species. It is precisely for such taxa that the subspecies category is so suitable.

# 2. CHANGES IN THE GENERIC CONCEPT

The excessive splitting of genera had already started in ornithology by the first half of the nineteenth century. By the 1920's a generic name was available for almost every good species (except sibling species). Even the slightest "morphological" difference between species was considered justification for the recognition of a separate genus. Only the fact that most geographic races were ranked as full species concealed the absurdity of this concept of the genus.

As the polytypic species was gradually being accepted and hundreds of morphological "species" were reduced to the rank of subspecies, a very large number of genera became monotypic. This assisted in a complete revision of the generic concept. It now became the function of the genus category to express relationship. By the time the fourth edition of the A.O.U. Check-list was published (1931), this shift of the generic concept had already made some progress and many previously recognized genera were then admitted only as subgenera, as in *Nyroca*, *Somateria*, *Melanitta*, *Buteo*, *Falco*, *Charadrius*, *Larus*, *Sterna*, *Vireo*, and *Carpodacus*, to mention only a few. This reconceptualization of the genus has progressed vigorously in the 39 years since 1931 and a count now shows that no less than 79 genera recognized in the 1931 list are combined by us with other genera of the 1931 Check-list. These are: *Morus* (= *Sula*), *Casmerodius* (= *Egretta*), *Dichromanassa* (= *Egretta*), *Hydranassa* (= *Egretta*), *Florida* (= *Egretta*), *Nyctanassa* (= *Nycticorax*), *Sthenel*-

ides (= Cygnus), Philacte (= Anser), Chen (= Anser), Chaulelasmus (= Anas), Mareca (= Anas), Dafila (= Anas), Nettion (= Anas), Querquedula (= Anas), Spatula (= Anas), Charitonetta (= Bucephala), Arctonetta (= Somateria), Oidemia (= Melanitta), Lophodytes (= Mergus), Astur (= Accipiter), Asturina (= Buteo), Canachites (= Dendragapus), Pedioecetes (= Tympanuchus), Lophortyx (= Callipepla), Oreortyx (= Callipepla), Pagolla (= Charadrius), Oxyechus (= Charadrius), Eupoda (= Charadrius), Squatarola (= Pluvialis), Phaeopus (= Numenius), Actitis (= Tringa), Heteroscelus (= Tringa), Totanus (= Tringa), Arquatella (= Calidris), Pisobia (= Calidris), Pelidna (= Calidris), Ereunetes (= Calidris), Crocethia (= Calidris), Steganopus (= Phalaropus), Lobipes (= Phalaropus), Pagophila (= Larus), Rissa (= Larus), Rhodostethia (= Larus), Xema (= Larus), Gelochelidon (= Sterna), Thalasseus (= Sterna), Hydroprogne (= Sterna), Endomychura (= Brachyrhamphus), Zenaidura (= Zenaida), Melopelia (= Zenaida), Scardafella (= Columbina), Scotiaptex (= Strix), Calothorax (= Archilochus), Calypte (= Archilochus), Centurus (= Melanerpes), Balanosphyra (= Melanerpes), Asyndesmus (= Melanerpes), Dryobates (= Picoides), Muscivora (= Tyrannus), Nuttallornis (= Contopus), Iridoprocne (= Tachycineta), Baeolophus (= Parus), Nannus (= Troglodytes), Telmatodytes (= Cistothorus), Catherpes (= Salpinctes), Corthylio (= Regulus), Limnothlypis (= Helmitheros), Chamaethlypis (= Geothlypis), Cassidix (= Quiscalus), Tangavius (= Molothrus), Spinus (= Carduelis), Pyrrhuloxia (= Cardinalis), Guiraca (= Passerina), Oberholseria (= Pipilo), Passerculus (= Ammodramus), Passerherbulus (= Ammodramus), Amphispiza (= Aimophila), Melospiza (= Passerella), Rhynchophanes (= Calcarius). Not all of these synonymies are universally accepted, but the trend is clear.

In addition the names of 17 genera have been changed because they were combined with genera outside North America. These are: Ajaia (= Platalea), Gymnogyps (= Vultur), Urubitinga (= Buteogallus), Philohela (= Scolopax), Columbigallina (= Columbina), Speotyto (= Athene), Antrostomus (= Caprimulgus), Nephoecetes (= Cypseloides), Megaceryle (= Ceryle), Ceophloeus (= Dryocopus), Xanthoura (= Cyanocorax), Penthestes (= Parus), Heleodytes (= Campylorhynchus), Ixoreus (= Zoothera), Cyanosylvia (= Luscinia), Acanthopneuste (= Phylloscopus), Hesperiphona (= Coccothraustes). The synonymizing of these 17 names did not lead to a reduction in the number of generic names employed in North America, but it did so on a world-wide basis. The mere change of a generic name for nomenclatural reasons, like Otocoris into Eremophila, is not included in the listing because it does not affect the generic concept and hence not the size of the genus.

Interestingly only two new genera are now admitted, Catharus and

Myioborus, both of them Central (or South) American genera, the North American species of which had been previously assigned to Hylocichla and Setophaga, respectively. Their recognition did not lead to an increase in the number of genera on a world-wide basis.

TABLE 8

NUMBER OF GENERA OF NORTH AMERICAN BIRDS

| Group   | Genera | Species |
|---------|--------|---------|
| Marine  | 17¹    | 40      |
| Α       | 34     | 77      |
| В       | 27     | 51      |
| С       | 32     | 86      |
| D       | 9      | 16      |
| ${f E}$ | 35     | 66      |
| ${f F}$ | 10     | 34      |
| G       | 48     | 86      |
| Н       | 48     | 151     |
|         |        |         |
| Total   | 260    | 607     |
|         |        |         |

<sup>&</sup>lt;sup>1</sup>Four additional genera of marine birds are listed under A and C.

The reduction in the number of recognized genera by 79(-2)=77 still leaves 260 genera for the 607 species (Table 8). In order to avoid misunderstandings, it is important to point out that many, if not most, of these genera have numerous species outside North America. It would be altogether wrong to say that North American genera of birds have an average of only 2.3 species. Nevertheless this figure indicates that the recent reduction in the number of recognized genera has not been excessive. Genera of birds are still rather finely divided.

## $\mathbf{V}$

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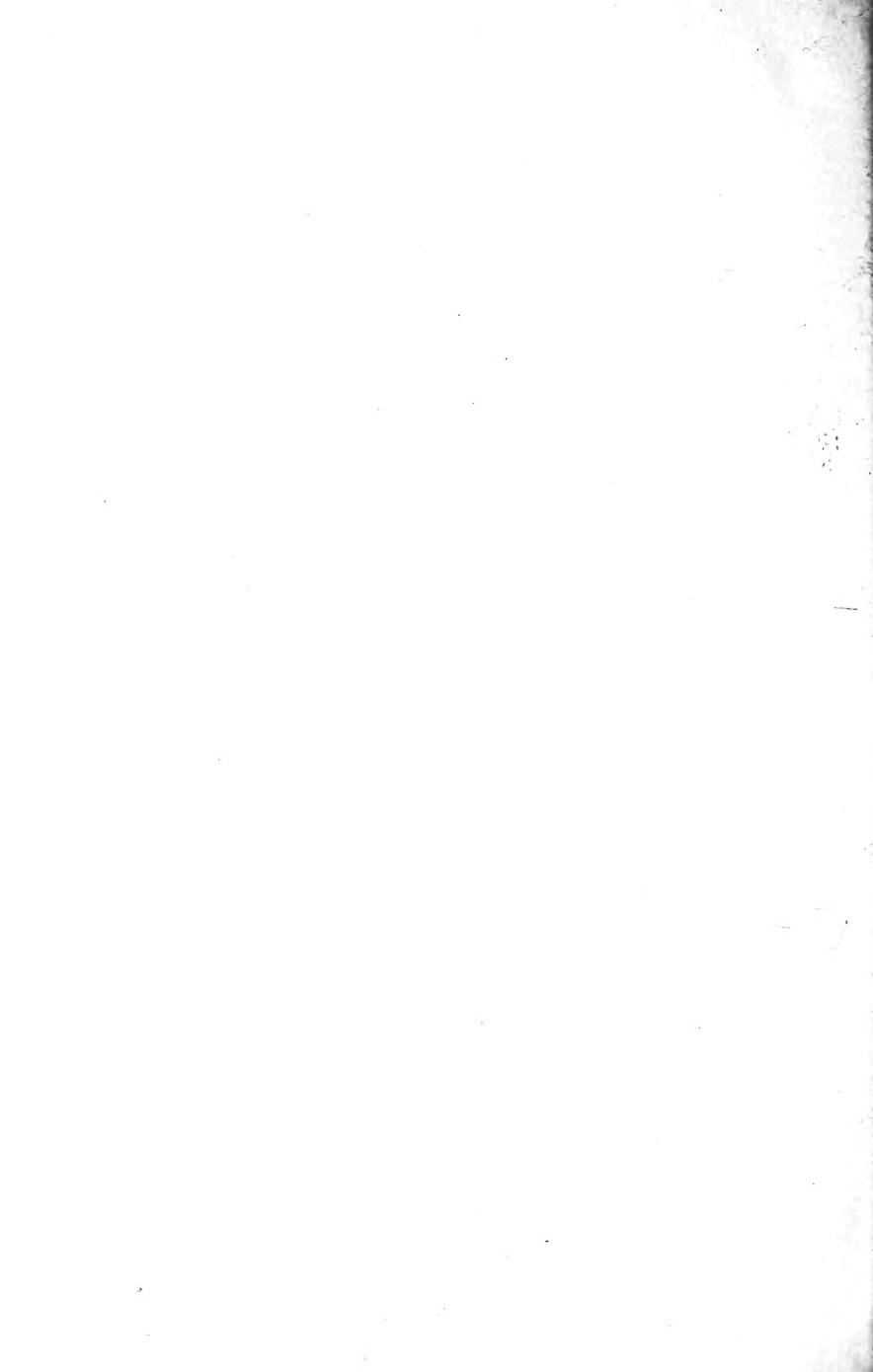
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